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MODELING THE FUTURE OF WOODLAND CARIBOU IN NORTHERN ALBERTA

by

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A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of Master of Science

in

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Faculty of Graduate Studies and Research

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled MODELING THE FUTURE OF WOODLAND CARIBOU IN NORTHERN ALBERTA submitted by Piotr Weclaw in partial fulfillment of the requirements for the degree of Master of Science   in Wildlife Ecology and Management.

ABSTRACT

Woodland caribou (*Rangifer tarandus caribou*) are classified as threatened in

Alberta. A variety of natural and anthropogenic factors that may impact caribou

populations act cumulatively in space and time. I developed a computer simulation

model REMUS as a tool for the assessment of these complex cumulative effects. The

model is based on functional and numerical responses of consumers to resources. It is

not fully deterministic (includes stochasticity) and is semi-spatial. Based on

simulation experiments I argue that in the natural boreal ecosystem: 1) caribou could

coexist with uncontrolled wolf (*Canis lupus*) populations that keep caribou at low

density; 2) habitat is not limiting caribou populations; 3) the most detrimental factor

on caribou population dynamics is the functional loss of habitat due to caribou

avoidance of good quality habitat in proximity of industrial infrastructures. I also

argue that wolf control is not a practical solution and discuss alternative management

options. To advance understanding of industrial impacts on caribou future research

should focus on the productivity of the ecosystem, the mechanism governing caribou

avoidance of industrial infrastructures, impact of other predators on caribou, and

caribou use of post-fire habitats.

ACKNOWLEDGEMENTS

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[1] The BCRP website: http://www.deer.rr.ualberta.ca/caribou/bcrp.htm

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CHAPTER I
GENERAL INTRODUCTION

1.1. Need for Caribou Conservation

There are two ecotypes of woodland caribou (*Rangifer tarandus caribou*) in Alberta: mountain woodland caribou (west central Alberta), and boreal woodland caribou (northern Alberta). Both exist at very low densities (Edmonds 1988, Fuller and Keith 1981, Stuart-Smith *et al.* 1997). Although it has been argued that there is not enough evidence to conclude that the observed low densities result from the long-term continued decline of the population (Bradshaw and Hebert 1996), there is a common belief that it has experienced significant decrease over the last decades (Edmonds 1988, Bergerud 1974, Bergerud 1988). Even more importantly, recent population monitoring suggests that most woodland caribou populations in Alberta are declining (Dzus 2001). Moreover, the caribou range in Alberta has shrunk significantly over time (Edmonds 1991). When an already small population declines and its range is reduced, there is a danger of this population falling to densities too low to ensure its viability.

To protect caribou populations from further decline, reasons need to be determined for the observed decrease in caribou density and, based on this knowledge, mitigation recommended. Here, the ability to assess the relative importance of factors shaping caribou dynamics and their interactions would be very helpful. Understanding how the caribou system functions and what its key components are, is fundamental. For successful management a holistic approach encompassing all major relations and links within the system is necessary. Management decisions that would result in the increase of the population growth are needed.

The concerns about the low density of woodland caribou led to threatened classification under the Alberta Wildlife Act in 1987 (Alberta Wildlife Management Division 1996). Industrial development continues on most caribou habitats in Alberta. To understand and hopefully mitigate the effects of industry, several initiatives were

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undertaken (Dzus and Boutin 1998, Hamilton and Edey 1998). In the early 1990s the Northeast and Northwest Regional Standing Committees for Woodland Caribou (NERSC and NWRSCC) were formed. In 1999 the two merged to form the Boreal Caribou Committee (BCC) (Dzus 2001). My study was done as a part of a broader research initiative conducted by the Boreal Caribou Research Program (BCRP)[1], a research group started in 1991 and operating under the BCC. The BCRP is a collaborative project involving partners from industry, government and university. Its goal is to generate scientific knowledge about caribou ecology, the boreal ecosystem and the effects of industrial activity on caribou. This information is used to integrate industrial land-use guidelines with caribou conservation.

1.2. Woodland Caribou Research in Northern Alberta

Significant research on caribou ecology in northern Alberta has been accomplished by the BCRP researchers. The first initiatives were started under the auspices of NERSC by Bradshaw (1994), Bradshaw *et al.* (1995) and Stuart-Smith *et al.* (1997) who studied caribou distribution in relation to different habitats. The researchers concluded that caribou selected peatland habitats over all other habitat types and avoided uplands (Stuart-Smith *et al.* 1997). Similar work was carried out by Anderson (1999) who examined habitat use and selection by caribou in the Athabasca and Red Earth caribou ranges. His results supported the conclusions of Bradshaw *et al.* (1995) and Stuart-Smith *et al.* (1997) that caribou select treed peatlands. Investigation of the use of habitat by caribou in northern Alberta continues (BCRP 2000).

Bradshaw *et al.* (1997) studied the effects of simulated oil and gas exploration on caribou movements and behavior. They found that human disturbance increased caribou movements and displacement. Consequently, one could hypothesize that the reduction in caribou range is caused not only by the actual loss of caribou habitat but also by caribou avoiding good quality habitats due to increased human activities or

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[1] The BCRP website: http://www.deer.rr.ualberta.ca/caribou/bcrp.htm

predation. Dyer (1999) and Dyer *et al.* (2001) supported this hypothesis. They studied caribou use of areas adjacent to various human developments (i.e. roads, seismic lines and oil wells) and found that caribou used those areas less than expected. Dyer (1999) and Dyer *et al.* (2001) reported maximum avoidance distances of 1000 m (around oil wells) and 250 m (roads and seismic lines). They stated that avoidance effects were highest during late winter and calving and lowest during summer, which could be associated with traffic levels. Dyer (1999) also found that roads constituted semi-permeable barriers to caribou.

Beside habitat degradation and loss, predation is another factor that can negatively influence population dynamics. It is widely accepted that caribou are limited by predation mainly by wolves (*Canis lupus*) (Bergerud 1988, Bergerud 1996, Edmonds 1988, Seip 1992) and it is known that wolves are the major cause of caribou mortalities in northern Alberta (Dzus 2001). Discussion on the effects of predation on prey populations continues (Holling 1959, Marshal 1997, Messier 1994, Seip 1991, Solomon 1949, Walters 1986) and many important questions remain unanswered (Boutin 1992).

In northern Alberta, caribou-wolf interactions were recently investigated by James (1999) and James and Stuart-Smith (2000). James (1999) found that caribou selection of fen/bog complexes results in spatial separation from moose that use upland habitats, and proposed that this separation in turn reduces predation pressure on caribou. James (1999) and James and Stuart-Smith (2000) also examined whether linear corridors increase predation on caribou, and found that animals that are closer to linear corridors are at higher risk of being killed by wolves. James (1999) also reported that wolves travel faster on linear corridors than in the forest. James concluded that industrial development on caribou habitat may potentially increase predation on caribou.

The findings of James (1999) and James and Stuart-Smith (2000) provide strong evidence that human-created linear corridors most likely affect caribou-wolf

interactions. There are also other ways in which humans may potentially disturb the natural balance of the caribou system. Among the most important are increased caribou mortality by hunting/poaching, and aforementioned reduction of habitat either by actual loss and fragmentation or by caribou avoiding good quality habitat in proximity of human built structures (Dyer 1999). Moreover, stochastic agents such as fire and extreme snow conditions have potential to negatively impact caribou population dynamics by reducing available habitat and forage as well as by decreasing animals' mobility that can in turn increase mortality due to predation.

1.3. Project's Objective

Consequently, there are a number of factors capable of shaping caribou population dynamics. The first and the most obvious one is natural habitat that provides animals with crucial resources such as food and space. If the species' natural habitat is lost usually the species is no longer able to survive. However, the sole protection of habitat, although crucial, may be insufficient to prevent the decline of the population if other factors prevent its growth. Textbooks on ecology teach us that a population will grow if the recruitment to the adult age class exceeds the mortality of adult animals (Begon *et al.* 1990, Caughley and Sinclair 1994). Conversely, a population will decline if the number of animals entering the reproductive age is smaller than the number of dying animals. Changes in those numbers will alter dynamics of the population. Habitat alteration, predation, forage availability and human harvest may negatively influence caribou population dynamics. All those agents act simultaneously in space and time.

The objective of my project was to evaluate the relative significance of the major factors (predation, habitat fragmentation and habitat loss, and forage) influencing caribou population dynamics. I identified thresholds for those primary factors shaping population dynamics either directly (e.g., increased density of predators) or indirectly (e.g., habitat alteration). These thresholds could be tested in field experiments.

A tool capable of assessing the cumulative effects of the key factors that shape caribou population dynamics would be very helpful in evaluating their relative importance. Based on the present understanding of caribou ecology and on recent research findings I developed a computer simulation model which might serve as a tool for the assessment.

1.4. Thesis Overview

This thesis is comprised of five chapters. The introduction (Chapter I) is followed by a detailed description of the model (Chapter II). I provide the internal structure of the model and references upon which it has been built. I also discuss its capabilities and limitations. Descriptions of all the controls available to the users of the model and the format of potential outputs are included in Chapter II.

In Chapter III, I assess at top-down (predator) and bottom-up (vegetation) forces in the caribou system. I simulate the natural conditions of the boreal ecosystem in northern Alberta when human impact on caribou was low (habitat is neither fragmented nor lost by human developments, and caribou are not hunted). Based on the outputs of the simulations I address the question whether the caribou system under natural conditions is controlled mainly by vegetation or predators.

In Chapter IV, I introduce human interaction into the natural caribou system and deal with the effects of human developments on caribou population dynamics. In the model, I simulate habitat loss due to physical destruction and functional loss due to reduced use by caribou of good quality habitat. In this way, I address the question of how human activities within caribou habitat affect the natural balance of the ecosystem simulated in Chapter III. I also attempt to assess the effects of increasing densities of linear corridors on wolf predation on caribou.

In Chapter V, I evaluate the model in relation to the major concerns in management in the boreal ecosystem with regard to caribou conservation (e.g. changes in moose density, wolf control, thresholds for linear corridors, etc.). On the base of the outputs of the simulations I identify research that could help to answer questions important in caribou conservation. I also discuss how the model and its application can be extended in the future.

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Chapter II
REMUS - WOODLAND CARIBOU DYNAMICS MODEL

2.1. Computer Simulation Modeling in Caribou Conservation

Using STELLA™ Research 6.0.1 modeling software (High Performance Systems Inc. 2000) I developed a systems dynamics model called REMUS. According to the ancient Roman legend, Romulus and Remus were twin brothers nursed by a female wolf. As Remus and Romulus were fed by a wolf, the model is based on information on the boreal ecosystem in which wolves (*Canis lupus*) are one of the key components. REMUS describes woodland caribou (*Rangifer tarandus caribou*) population dynamics in northern Alberta in response to two major groups of factors: 1) natural (predation, forage availability, fire, and snow conditions) and 2) human-induced (human harvest and habitat alteration/loss). The model operates in MS Windows 98™ (or higher) environment and its interface enables a person familiar with MS Windows™ to run the model without any knowledge of STELLA™ Research software. I incorporated into the model a tutorial that explains how to run and operate the model. Using STELLA™ as the modeling tool makes the model compatible with other models already developed or being developed in the Boreal Caribou Research Program (BCRP).

The goal of any model is to help to understand how the described system functions. A model is an attempt to fit all the elements interacting in the system together and to estimate their place in the overall picture of the dynamic entity. The more parts of the system that are described with data driven from actual field experiments, and the more detailed these descriptions are, the more precise prediction one is able to make using the model. If some elements are blank due to the lack of information on specific subjects, the model helps to identify those gaps. As stated by Starfield (1997), the ultimate test of a model is not how accurate or truthful it is, but whether it informs the decision-making process.

By simulating specific conditions in a model, one can test hypotheses. However, as every model is a virtual image of the real world, it is a hypothesis itself. Large models built as computer programs involving numerous interactions provide their users with tools with which to formulate critical hypotheses.

There are also other reasons for employing computer modeling in ecology. First, models are helpful in predicting the dynamics of the systems before costly actions are undertaken. Moreover, by predicting future events, modeling helps managers choose the best management and conservation strategies (Finley 1998, Messier 1994, Montopoli and Anderson 1991). Modeling is also used in studies where the scale (temporal or spatial) is too large for effective experiments (for example long-lived organisms, processes that act in global biosphere). Numerical models are employed where actual manipulation of the populations examined may be impractical or illegal (endangered species). Finally, modeling is important because it helps to plan ahead and avoid environmental damage (Spaling and Smit 1995). Because assessment of several effects acting cumulatively is expensive (examination of different aspects of the ecosystem usually involves several research projects), modeling is even more important.

Modeling at different scales is one of the current research initiatives being conducted in the BCRP. The first is landscape habitat modeling. Dr. Brad Stelfox has developed a model called A Landscape Cumulative Effects Simulator (ALCES™) that tracks the accumulating changes to habitat and allows comparison of the relative effectiveness of various future land use policies and practices.

The second level of modeling is done at the population level and is accomplished in my work. Merging the models documenting industrial activity, caribou habitat use and caribou population dynamics would result in a comprehensive cumulative effects simulation model that could be used as a tool to assess various land development scenarios and their consequences on caribou population.

REMUS has a potential to simulate a variety of scenarios and their impact on caribou dynamics. However, for this thesis I narrow my focus to examine the effects of several factors as outlined in the next section of this chapter.

2.2. Overview of REMUS

The model is designed as a dynamic system that can be adjusted if new data becomes available and if the present understanding of caribou ecology changes. The ease of manipulating the elements of the model, makes it a flexible tool capable of being adjusted to examine different areas and populations that inhabit them. In this chapter I provide description of the model interface (section 2.5), internal structure of the model, and its default settings (section 2.3). In chapters 3 and 4, I give model settings used for particular simulations.

Extensive research accomplished in the BCRP allowed me to build a computer simulation model (REMUS) describing caribou population dynamics. Although the BCRP research was the main source of information for REMUS, literature relevant to caribou and the boreal ecosystem was consulted to fill gaps. Extensive reviews based on several studies (e.g. Messier 1994) were preferred to studies from one location different than Alberta (e.g. Hayes *et al.* 2000) Expert opinion of researchers having extensive experience on boreal ecology was also important in the decisions made when building the model.

As time and space are the two characteristics that anchor any work, REMUS has its own spatial and temporal attributes.

Space. The model is semi-spatial and assumes that there are two types of habitat in the simulated area: lowlands (fen/bog peatland complexes dominated by black spruce (*Picea mariana*) and tamarack (*Larix laricina*); and uplands (well-drained areas, abundant with aspen (*Populus tremuloides*), white spruce (*Picea glauca*) and jack pine (*Pinus banksiana*), see Anderson (1999) and Bradshaw *et al.* (1995) for a detailed description). The proportion of lowlands and uplands and the size of the total area can be adjusted by the user depending on simulation needs.

The model is not spatially explicit and as such does not account for relative distribution of patches of lowlands and uplands. Anderson (1999) and Bradshaw *et al.* (1995) reported that caribou select lowlands, whereas moose (*Alces alces*) use mostly upland habitats (James 1999). The model assumes that lowlands are used by caribou, and moose use uplands. Wolves penetrate both habitat types. The model does not reflect the distribution of animals within their selected habitat in relation to landscape features (e.g., lakes, rivers). However, the fact that wolves use uplands more than lowlands (James 1999) is reflected in the model by wolves selecting moose (James 1999) as their prey species (section 2.3.3). Reduced use of areas adjacent to human-built structures by caribou is included in the model (section 2.3.8.1).

The unit of measurement in the model is 1 km^2. The model assumes that there is no immigration into the system. Thus, setting the initial density of a particular species to zero is equal to the exclusion of the species from the system. Similarly, the decline of any of the populations to zero means its permanent disappearance.

Time. Management of species capable of producing young every year and only once in a year should focus on yearly changes in population dynamics. The dynamics of woodland caribou in northern Alberta is monitored on a yearly basis by the BCRP (2000). Similarly, the unit of time in REMUS is one year. However, important changes in caribou population dynamics are not distributed evenly over time. Caribou calves are born usually in May and the majority of them within one month (BCRP 2000). Consequently, the time step of the model (a unit of time after which all calculations are computed) is one month. Simulation time is expressed in years and may be set by the user from a 1-year simulation to any duration (in full years) desired by the user. To reflect seasonal characteristics of the boreal ecosystem, the model includes seasonal variations in forage availability (plants) and accessibility (lichen) to caribou.

REMUS includes stochasticity. As random events are present in real world situations, it is important to include them in simulation models. Random number generators are incorporated into four elements of the model: fire, snow conditions, bear predation and human harvest.

2.3. Internal structure of the model

The model is built (Figure 2.1) as an ecosystem with three trophic levels: 1) producers: caribou forage (divided into lichens and vascular plants), moose forage; 2) primary consumers: caribou and moose; 3) secondary consumers: wolves, black bears and humans.

As illustrated in Figure 2.2, I model caribou responses to two main groups of cumulative effects: 1) natural and 2) anthropogenic factors. Consequently, the model consists of the following main sectors: 1) caribou population; 2) caribou forage (lichens and plants); 3) predation (wolves and black bears); 4) moose population (including moose forage); 5) human harvest; 6) fire; 7) snow; and 8) habitat loss.

2.3.1. Caribou Population

The model considers two aspects of caribou population characteristics: age structure and gender. The caribou population is partitioned into three pools: calves, yearlings and adults. Simultaneously, each pool is further divided for males and females. As suggested by BCRP (2000) around 50% of the documented adult female caribou deaths are due to wolf predation. It is also known that black bears prey on caribou (Ballard 1994). Another 8% of adult female mortalities are human-induced and next 29% of mortalities are due to unknown causes. Consequently, the model assumes that there are four causes of caribou mortality: 1) possible food limitation, 2) wolf predation, 3) bear predation, and 4) human harvest. If caribou density becomes higher than the carrying capacity of the ecosystem determined by forage availability, the caribou population will decrease due to reduced fecundity resulting from food

shortage. If there is no predation or human harvest, caribou stabilize around the carrying capacity of the system determined by forage availability. The model assumes that all calves are born in May (BCRP 2000).

In the model, caribou population dynamics are determined by changes in birth rates, survivals and mortalities (Figure 2.3). If survival exceeds mortalities the population grows, otherwise decline is observed. The equation for birth rates is based on Michaelis-Menten kinetics (Segel 1993):

$$y = a * ((f / (f + h)))$$ C.1

where:
y – number of newborn calves;
a – number of females;
f – forage available;
h – caribou foraging efficiency.

I assume that the initial amount of forage (parameter f) is equal to the forage carrying capacity of the system that can be specified by the user of the model (section 2.5). The values for caribou forage carrying capacity are based on data presented by Thomas and Kiliaan (1998), (section 2.3.2). Foraging efficiency (h) is the biomass of available forage at which caribou food intake rate is equal to half of the maximum intake rate (Figure 2.4). From the data presented by Trudell and White (1981), the value of the parameter h can be calculated to be 40 g/m^2 for lichens, and 30 g/m^2 for vascular plants. Adjusting these numbers for the unit of area used in the model, the values of parameter h are 400 kg/ha or 40 000 kg/km^2 for lichens, and 300 kg/ha or 30 000 kg/km^2 for vascular plants.

Based on the equation C.1 a specific number of calves is born in a period of one month. Next, they can die because of malnutrition or predation. The equation for food limitation-caused mortality is:

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$$y = a * (1 - f / (f + h))$$ C.2

where:

y – number of animals dying;

a – numbers of animals in the population;

f – forage available;

h – caribou foraging efficiency.

The equations C.1 and C.2 are adjusted for the relative importance of plants and lichens in caribou diet. According to Bergerud (1972), vascular plants constitute around 35% of the total caribou diet.

The equation for wolf predation is:

$$y = w * e * a / (a + d)$$ C.3

where:

y – number of caribou killed by wolves;

w – the density of wolves;

e – the asymptotic killing rate when wolves are fully satiated (section 2.3.3);

a – the caribou density;

d – predator's efficiency (the caribou density at half the maximum killing rate (section 2.3.3)).

The second natural predator included in the model is black bear (*Ursus americanus*). The model assumes that a certain proportion of caribou are taken by bears annually and random number generator gives ± 1.5% variability around this number specified by the user of the model at the start of the simulation. Consequently, bear predation is described:

i = a * m * random   C. 4

where:

i – number of caribou depredated by black bears;

a – caribou density;

m – proportion of the population killed by black bears annually;

random – random number generator that produces ±1.5% variability around

m

Surviving calves (neither killed by natural predators nor dead of starvation) enter the yearling age class. Similarly as calves, yearlings can die because of potential food shortage or be killed by predators. Consequently equations C.2, C.3 and C.4 apply to yearlings. In the model, yearlings can be also poached or hunted. The following equation gives the number of caribou killed.

j = a * n * random   C.5

where:

j – number of caribou killed by people;

a – caribou density;

n – proportion of the population killed by people;

random – random number generator that produces ±1.5% variability around

n.

Surviving yearlings are recruited to the adult pool. As adult animals can potentially die because of food shortage, predation or human harvest, equations C.2, C.3, C.4 and C.5 are applied to the adult pool. The model assumes that there is equal sex ratio among adult caribou. Adult females give birth to calves once a year according to equation C.1. Yearlings do not reproduce in the model.

2.3.2. Caribou Forage – Lichen and Plants

The elements of herbivore-forage dynamics such as forage availability and forage growth rates determine what potential densities of caribou could be sustained by the boreal ecosystem. This potential is one of the key issues in caribou conservation. When designing the forage component of the model I decided to bias it toward showing caribou densities lower rather than higher.

Caribou utilize different kinds of forage. Although they can feed on evergreen shrubs in winter, and a variety of other vascular plants in summer, caribou are lichen specialists and feed mainly on lichens *(Cladina* spp.*, Cladonia* spp.*, Usnea* spp.*)* (Bergerud 1972, Fuller and Keith 1981, Thomas 1995). Therefore, the model includes two pools: 'lichens' and 'plants' as a total caribou forage.

Other reasons for dividing caribou forage into two pools are: different growth rates specific for lichen and vascular plants with the latter having much higher growth potential; and differences in seasonability with lichens being available to caribou year round and green biomass of vascular plants available mostly in summer.

The model describes forage dynamics assuming that there is a specific carrying capacity in the system (specific area supports a given maximal amount of biomass). Forage growth is density dependent. The general equation for forage growth is:

$$y = s * f * (1 - f/f_k) \qquad \text{F.1}$$

where:
y – the annual increment (kg/km^2);
s – the maximum growth potential;
f – the amount of forage in the system;
f_k – forage carrying capacity of the system (the maximum amount of forage

that the system can sustain).

Different growth rates of lichens reported in literature are presented in Table 2.2. The most detailed description of lichen growth rates is given by Gaare (1997). According to his work lichen growth is density dependent. Gaare (1997) reports the highest growth potential to be 20% of the present biomass if it is low. The higher the value of parameter **s** in the model, the higher the potential of the habitat to sustain high-density caribou populations. To bias the model towards showing low caribou carrying capacity of the system, by default setting the model assumes the maximum growth potential for lichen (**s**) to be 7% (s = 0.07). Used in simulations, this value results in complete regeneration of a burned site in 60 years. Based on values reported by Gaare (1997) it could be expected that the actual maximum growth potential for lichen in natural conditions is almost three times higher. The design of the model allows its users to adjust the value of parameter **s** according to simulation needs (section 2.5).

Vascular plants have much higher growth potential. Using 0.5 as the value of the parameter **s** for plants means that they can fully recover in two years after (over)browsing (Bergstroem and Danell 1995, Danell *et al.* 1985).

The initial value of parameter **f** (the amount of forage in the system) is set at the carrying capacity of the system. Next, due to fires and potential overgrazing, as well as due to forage growth, the amount of forage available changes dynamically over time. By default I use 870 kg/ha for lichen carrying capacity of the lowlands. This is a low estimate for terrestrial lichens in the boreal ecosystem (Table 2.1). As this is the actual amount of lichen biomass measured in the field, the lichen carrying capacity of the system is probably more than that.

Reliable information on the biomass of vascular plants available to caribou on lowlands is not available. Different values of green plants availability are reported for habitats other than peatland complexes (Table 2.3). Based on this evidence it could be

assumed that the amount of plants available to caribou on lowlands is lower than 533 kg/ha. By default, the model uses 240 kg/ha that is around 45 % of the lowest value reported by Wickstrom *et al.* (1984). Accounting for the fact that caribou could occasionally forage on uplands rich in green forage, I believe that the above value is a conservative estimate. Using the aforementioned low estimates for lichens' and vascular plants' availability and assuming that these are the carrying capacities for both kinds of forage biases the model toward showing low potential of the system with respect to caribou density.

Three factors contribute to lichen depletion: fire (see section 2.3.6), habitat loss (see section 2.3.8.1), and consumption by caribou. The equation for forage consumption is as follows:

$$y = a * l * f / (h + f) \hspace{4cm} F.2$$

where:
y – total annual consumption,
a – density of animals,
l – annual forage requirement by an individual caribou;
f – forage available;
h – caribou foraging efficiency.

Based on the data reported by Hanson *et al.* (1975) and Holleman *et al.* (1979), the value of parameter **l** is set to 5% of caribou body weight per day by the default settings of the model.

2.3.3. Predation

In the boreal forest in Alberta, a number of predators can have an impact on a caribou population. Wolves *(Canis lupus)*, grizzly *bears (Ursus arctos)*, black bears *(Ursus americanus)* and lynx *(Lynx lynx)* all are capable of killing either adult caribou

or calves. Several studies suggest that wolves are the main predators for caribou (Bergerud and Elliot 1986; Bergerud and Ballard 1989; Edmonds 1996; Fuller and Keith 1981; Seip 1992; Thomas 1995) and the natural factor that may limit caribou populations. As suggested by BCRP (2000) wolves contribute to about 50% of the documented caribou deaths. Although it is also known that black bears prey on caribou, black bear predation on caribou in North America has not been reliably quantified (Ballard 1994). Another 8% of all mortalities are human-induced and in 29% of all cases of mortality the cause was impossible to determine (BCRP 2000). Accordingly, two natural predator species are included in the model: wolves and black bears.

Wolf population dynamics are driven by the abundance of its prey species, mainly moose and the secondary prey caribou. As wolves are territorial, the model assumes that even at very high prey densities wolf numbers will not exceed a certain level.

The reaction of a predator population to different prey densities can be described by predators' numerical and functional responses. The change in a predator population through reproduction, immigration and emigration is called the predator's numerical response (Caughley and Sinclair 1994). The functional response is defined as the relationship between a predator consumption rate of prey and the density of those prey (Begon *et al.* 1990).

Numerical response of wolves. In the model, the equation for the numerical response of wolf population dynamics is as follows:

Wolves(t) = Wolves(t - dt) + (WolvesGrowth) * dt   P.1

where:
Wolves(t) = wolf population at time t_1
Wolves(t - dt) = wolf population at time t_0

WolvesGrowth = change in wolf population in $t_1 - t_0$ time interval

$dt = t_1 - t_0$

and

WolvesGrowth = Wolves * r P.2

where:

Wolves - density of wolves expressed as individuals/km^2;

r – the annual rate of increase/decrease of the wolf population.

Bayliss (1987) has shown that the numerical response of consumers to resources can be described by a model similar to Michaelis-Menten model (Segel 1993). To describe r I use a modified Michaelis-Menten model. I assume that r is a function of prey density (Figure 2.5) that can be described by the following equation:

$r = - a + b * c/(d + c)$ P.3

where:

r – exponential rate of increase of the population;

a – the maximum rate of decrease (value of r when prey density is zero);

b – the upper limit of r;

c – density of prey expressed as individuals/km^2.

d – density of prey at which the kill rate is equal to half of the maximum kill rate (Figure 2.6). I call this variable "*predator efficiency*".

And, **$b - a = r_m$**, which is the maximum rate of increase.

Incorporating P.3 into P.2, results in the following:

WolvesGrowth = Wolves * (- a + (b * c)/(d + c))   P.4

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Therefore, at any time (t), the number of wolves is calculated:

Wolves(t) = Wolves(t - dt) + ({Wolves*(- a + (b * c)/(d + c)}) * dt   P.5

This requires the initial density of wolf population and values of **a**, **b**, **c** and **d** parameters.

Calculation of **a**. Let $r = 0$ in P.3, then

- a + (b * c_0)/(d +c_0) = 0   P.6

then

a = (b * c_0)/(d + c_0)   P.7

where:

c_0 – density of prey species at which $r = 0$, expressed as individuals/km^2

and

b – a = r_m   P.8

Calculation of **b**. The parameter r_m is the maximum growth potential of the population given unlimited access to food. Hayes and Harestad (2000*a*) reported wolf population increase from 29 to 245 wolves in 7 years. The rate of increase varied depending on wolf density and reached the highest value of 2.38 at very low density. Almost the same value (2.40) for the maximum annual rate of increase is given by Ballard *et al.* (1987). Other authors (Bergerud and Ballard 1989, Bergerud and Elliot 1998, Fuller 1989, Pletscher *et al.* 1997) report lower values for growth rates of wolf populations. Because the highest value of wolf population increase comes from the study by Ballard *et al.* 1987, and Hayes and Harestad (2000*a*) I use this number for the r_m parameter in the model. If $\lambda = 2.40$ and $ln\lambda = r$, then $r = 0.875$.

r_m = b - a = 0.875   P.9

then,

$b = 0.875 + a$ P.10

Substituting P.10 into P.7 gives:

$a = ((0.875 + a) * c_0) / (d + c_0)$ P.11
Then,
$a = 0.875 * c_0 / d$ P.12

Calculation of c_0. From a study done in southwestern Quebec, Messier (1987) reported that wolves were nutritionally stressed when moose density decreased below 0.4 moose/km^2. Messier (1985) believes that moose density = 0.2 moose/km^2 represents the threshold density below which wolves cannot reproduce successfully or subsist if there is no alternate prey species. Then:

$c_{0moose} = 0.2$ **moose/km**^{2} P.13

Calculation of **d**. Messier (1994) describes the functional response of wolves by the hyperbolic Michaelis-Menten function:

$y = e * c / (d + c)$ P.14

where:
y – number of moose killed per wolf per 100 days;
e – the maximum killing rate (the asymptotic killing rate when wolves are
        fully satiated);
c – the moose density;
d – the moose density at half the maximum killing rate.

The parameter **d** in P.3 is equivalent to **d** in P.14. Messier (1994) reports that **d** = 0.46.

$d_{moose} = 0.46$ P.15

Substituting P.13, and P.15 into P.12, the value of the parameter **a** for moose can be calculated: $a_{moose} = 0.875 * 0.2 / 0.46 = 0.38$

$a_{moose} = 0.38$ P.16
and using P.10:
$b_{moose} = 1.255$ P.17

Assuming an average body weight of 147kg for caribou and 434 kg for moose (Stelfox 1993), the parameter c_0 for caribou can be calculated as follows:
$434/147 = 2.95$
$c_{0caribou} = c_{0moose} * 2.95$
$c_{0caribou} = 0.59 \text{ caribou/km}^2$ P.18

And $a_{caribou} = 0.875 * 0.59 / 4.6 = 0.112$

$a_{caribou} = 0.112$ P.19
and
$b_{caribou} = 0.987$ P.20

To account for the fact that in northern Alberta caribou are killed by wolves ten times less than their relative availability (James 1999), and assuming that $d_{moose} = 0.46$,

$d_{caribou} = 4.6$ P.21

The total numerical response of wolves is the weighted average of the sum of equations for moose and caribou.

Functional response of wolves. Functional response of a predator is the relation between the predator's consumption rate and prey density. To describe the functional response of wolves to prey availability in the model I use the modified Michaelis-Menten model as proposed by Hayes and Harestad (2000*b*) and Messier (1994). This is the equation P.14 presented above. I use different values of **d** and **e** parameters for moose and caribou. Messier (1994) proposes **d** = 0.46 and **e** = 3.36 for moose. A different value of **d** (d = 0.07) and similar value of **e** (e = 2.97) are proposed by Hayes and Harestad (2000*b*). Hayes and Harestad (2000*b*) argue that Messier (1994) underestimated the wolf kill rates at low moose densities, but it is also possible that those differences are due to different locations where data were obtained (Hayes pers. comm.). Taking the average of 3.36 and 2.97 and adjusting it for a year gives e_{moose} = 11.55 (after rounding e_{moose} = 12). Consequently, the equation for functional response of wolves to moose density takes the following form:

$$y_{moose} = 12 * x_{moose} / (0.46 + x_{moose}) \hspace{3cm} P.22$$

where:

y_{moose} – number of moose killed per wolf per year;

x_{moose} – the moose density

To reflect the fact that the functional response of wolves to caribou density may be different the above equation needs to be adjusted for caribou. Dale *et al.* (1994) gives the asymptotic value for kill rate to be 0.1 for a day. Therefore, for a year $e_{caribou}$ = 36.5 (e = 37 after rounding). The difference in values of **e** for moose and caribou reflects the difference in caribou and moose body weights. To account for the fact that in northern Alberta caribou are killed by wolves ten times less than their relative availability in habitat (James 1999) the model uses $d_{caribou}$ = 4.6. Wolf functional response to caribou is described as follows:

$$y_{caribou} = 37 * x_{caribou} / (4.6 + x_{caribou}) \hspace{3cm} P.23$$

where:

y – number of caribou killed per wolf per year;

x – the caribou density.

The above values of parameters **d** and **e** are used by the default model settings. The design of the model allows using other values of the parameter **d** according to simulation needs (the user can adjust it at the start of the simulation). The parameter **d** for caribou may be influenced by linear corridors (section 2.3.8.2). The value of parameter **e** is adjusted in the model according to the design of wolves' social behavior.

Social behavior of wolves. An important element of wolf population dynamics is territorial and social behavior of wolves. The size of a territory and number of wolves in a pack determine the maximum potential density of wolves, which in turn establishes certain predation pressure on ungulate populations. Generally, it is believed that the size of a territory is a compromise between acquiring more benefits from large territory and reducing costs associated with its defense (Gass *et al.* 1976). Territory size may vary depending on a number of factors (e.g., prey density and/or biomass, number of individuals in a pack (Ballard *et al.* 1987, White *et al.* 1996)). It is known that the density of prey affects the size of wolf territories (Wydeven *et al.* 1995). Nevertheless, one can expect that there is some upper threshold wolf density due to wolves' social behavior shaped over time by evolution. Ballard *et al.* (1987) list wolf densities from 26 different studies. The highest reported density is 128 wolves/$1000km^2$ when wolves were artificially introduced to an island (Coronation Island, Alaska). According to Ballard *et al.* (1987) the highest reported wolf density in natural conditions was 56 wolves/$1000km^2$ in Northwest Territories. There is significant variation in the reported wolf territory sizes (Ballard *et al.* 1987, Okarma *et al.* 1998, Messier 1985, Wydeven *et al.* 1995). Gunson (1992) reports average territory size for wolves in northern Alberta to be 919 km^2. This value is used by the default settings of the model and can be manipulated by the users of the model in the range from 700 to 1200 km^2.

Another important characteristic of wolf populations is wolf pack size. Gunson (1992) states that the average size of a wolf pack in Alberta is 8.7 wolves; however, the number of wolves in a pack is not constant and may differ between packs and years (Hayes and Harestad 2000*a*). Different factors can potentially determine the optimal pack size in social carnivores (Caraco and Wolf 1975, Nudds 1978). More importantly, it has been shown that kill rates per one wolf depend on pack size and are lowest for wolves in large packs (Hayes and Harestad 2000*b*, Hayes *et al.* 2000). Consequently, food acquisition per wolf declines with an increase in pack size (Schmidt and Mech 1997, Thurber and Peterson 1993). Then, the combination of the size of a territory (affects the density of wolves) and the number of wolves in a pack (affects the density of wolves and kill rates) has important consequences on wolf predation pressure, which does not change linearly with changes in wolf densities. This is reflected in the model by the equation for wolf kill rates in response to pack size ($log_{10}y = 0.93 - 0.03x$, where y is the number of moose killed per wolf per day, and x is the number of wolves per pack (Hayes *et al.* 2000)) that modifies wolf functional response equation (P.14) by adjusting the maximum kill values.

In the model, a control that allows its users to examine the effects of simulated prey switching (Begon *et al.* 1990, Bergerud 1983) has been implemented. The design of this component assumes that if prey switching is in ON position, wolves will always select the species that is more abundant in the system (the value of the parameter **d** will be lower for the selected species).

The second natural predator species in the model is the black bear (*Ursus americanus*). Evidence exists that black bears prey on woodland caribou (Ballard 1994). Due to the lack of detailed information on black bear predation on caribou in Alberta the model employs the most parsimonious mechanism to describe the effects of black bear predation on caribou. Equation C.4 gives the number of caribou killed by bears annually. The user can specify the percent of animals from each age class

taken by bears every year (parameter **m** in C.4). This number is next adjusted during the simulation by a random number drawn from normal distribution. The random factor implements 3% variability around the number specified by the user. For example, if the user sets the bear predation to 10%, this will result in black bear predation in a range from 8.5 to 11.5% of caribou during the simulation.

2.3.4. Human Harvest

Data suggest that human harvest is one of the causes of caribou mortality in Alberta (Dzus 2001). Also, it could be hypothesized that at least some portion of the 'unknown causes' is due to humans. Recreational hunting of caribou stopped in Alberta in 1981, consequently one can distinguish two categories: hunting by the First Nations and poaching. In most cases it is not possible to determine whether the animal was poached or taken legally by Aboriginal hunters. Therefore, I include all human-caused mortalities in one pool called 'human harvest'. The number of caribou killed by humans is given by the equation C.5 (section 2.3.1). The model allows its user to specify the percent of caribou population culled by humans annually (parameter **n**). Next, this number is modified by a random number from a normal distribution to reflect stochastic changes in poaching and hunting pressure.

2.3.5. Moose Population

Moose (*Alces alces*) are the staple prey for wolves in northern Alberta (Bergerud 1974, James 1999) and it has been proposed that high moose numbers result in high wolf population densities, which in turn increases predation on caribou (Bergerud 1974, 1985, Bergerud and Elliot 1986, Fuller and Keith 1981, Seip 1991). Therefore, moose population is included in REMUS. In the model moose utilize the upland portion of the total area simulated. The approach in the design of the dynamics of moose population is the same as for caribou (see section 2.3.1). The differences are following: 1) the model assumes three causes of moose mortality: potential food limitation, wolf predation and hunting; 2) moose population is partitioned into two

age classes: young moose and adult moose. Young moose are animals younger than one year.

Consequently, modified equations C.1, C.2, C.3 and C.5 are used to describe moose dynamics. The important factor in determining moose population dynamics is the maximum carrying capacity of upland habitats for moose. Telfer and Scotter (1975) estimate moose carrying capacity of moose in Elk Island National Park (EINP) to be 4.4 moose / km^2. Similar values are given by Blyth (1995) who reports fluctuations in moose density in EINP in the range from 1 to 8 moose / km^2. In Newfoundland, in good quality habitat moose density fluctuated in the range 1.1 – 4.6 moose / km^2 (Bergerud and Manuel 1969). Telfer (1984) believes that coniferous/deciduous transition ranges in boreal region may support moose densities in a range of 1 to 3 moose / km^2.

Using values for moose foraging given by Renecker and Hudson (1986), and the amount of biomass (1351 – 1752 kg /ha) reported by Renecker and Hudson (1986) from Ministik Field Station southeast of Edmonton, produces moose densities around 4 animals / km^2, the same as that reported for EINP (Telfer and Scoter 1975, Blyth 1995). The potential of upland habitats in northern Alberta is most likely lower than that of areas close to Edmonton. Consequently, lower biomass of moose forage needs to be used in model simulations. Biomass of forage around 970 kg/ha produces in simulations moose population that stabilizes at the density of 3 moose / km^2 in upland habitat. This is the maximum carrying capacity of uplands used in the model. The density per total area including lowlands will be lower depending on the proportions of lowlands and uplands in the simulated area. It could be hypothesized that the actual moose densities are lower due to predation and hunting that can be simulated in the model.

2.3.6. Fire

Bradshaw and Hebert (1996) report that the total area burned per year in

Alberta from 1918 to 1979 has never exceeded 1.2% of the total forested area. However, fires are not randomly distributed in landscape. Different kinds of vegetation have specific probabilities of being burned (Cumming 2001). According to Cumming (2001) the annual burn rate for wetlands in the Alberta boreal mixedwood is 0.17% and including all vegetation classes the average annual rate of burn is 0.21%. This is consistent with values reported by Ehnes (2000) who states that 50% of treed peatlands are skipped by fires in Manitoba. Bergerud (1971) reports that it takes over 25 years for terrestrial lichens to recolonize burned sites. Thomas and Kiliaan (1998) report that stands become productive in terms of caribou forage as early as 40 to 50 years after fire and that biomass of lichens stabilizes in 60 years after fire. Then, it can be assumed that habitat becomes fully regenerated for caribou in terms of lichen biomass in less than 60 years after fires. Based on the above evidence one can calculate what on average would be the proportion of the lowland areas not suitable for caribou to forage.

$$p = y * t * b \qquad\qquad R.1$$

where:

p – proportion of caribou habitat that is unsuitable for caribou foraging;

y – number of years needed for lichens to regenerate;

t – proportion of the total area burned annually;

b – probability of burning for peatlands when the average probability of burning for the total area is expressed as 1

Using the high estimates from Bradshaw and Hebert (1996), Ehnes (2000) and Thomas and Kiliaan (1998), equation R.1 can be solved:

$$p = 60 * 1.2 * 0.5 = 36 \qquad\qquad R.2$$

This assumes that stands younger than 60 years do not burn. Such a supposition is unrealistic. Moreover, habitat becomes suitable for caribou in less than

60 years. Then, the percent of caribou habitat not suitable for foraging is much less than 36% calculated in R.2.

Using numbers reported by Cumming (2001), the equation R.2 can be solved:

$$p = 60 * 0.17 = 10.2 \hspace{4cm} \text{R.3}$$

In the model, I assume that the maximum area not suitable for foraging due to fires may be up to 25% of the total lowland area and that this area is never less than 12% with an average of 18%. At a large scale, fire is not fully random with some habitats having higher probability of being burned than others (Cumming 2001). However, within the specific habitat types the relative importance of stochastic ignition is greater. To simulate the stochasticity in fire occurrence within caribou habitat, random number generator produces the variability in the area burned around the average of 18% and with lower boundary set at 12%, and the upper boundary set at 25%. Considering that fire suppression may further reduce the number of fires in future, and that caribou can potentially forage in uplands, I believe that the above estimation is biased towards showing smaller potential of the habitat for caribou carrying capacity.

The fire component may be switched OFF or ON. When fire is in the OFF position no area is lost for caribou due to fires.

2.3.7. Climate – Snow Conditions

Severe winters and cold temperatures do not seem to be the direct cause of caribou mortality (Bergerud and Elliot 1986, Thomas 1995). Some researchers (Adamczewski *et al.* 1988, Brown and Theberge 1990, Kelsall and Telfer 1971, Thomas 1995) point out that snow conditions play important role in caribou population dynamics. Deep snow cover may not only obstruct mobility (Schneider *et al.* 2000, Stuart-Smith *et al.* 1997) by making them more vulnerable to predation but also affects caribou' energy budgets as it requires more energy to move in deep snow

and to search for food under thick snow cover. Hypothetically unbalanced energy budgets would in turn affect the overall condition of animals increasing their vulnerability to predation. Also, by weakening cows' conditions snow regime can indirectly influence calf survival (Adams *et al.* 1995, Cameron *et al.* 1993, Thomas 1995) or in extreme cases result is miscarriages and prolonged infertility.

The model has a potential to simulate the effects of snow on caribou access to food resources and caribou movements, which may affect predation rates. The user of the model specifies the maximum snow depth in winter. As snowfall is a stochastic variable, a random number from a normal distribution alters the maximum snow depth provided by the user giving 5 cm variation around the value entered by the user. For example, if the user sets the maximum snow depth to 50 cm, it will vary throughout the simulation from 45 to 55cm. Another control called "**reduced_use**" allows the user to decide how the specified maximum snow depth reduces caribou access to food. Although different authors describe the potential effects of snow on caribou populations (Adamczewski *et al.* 1986, Adams *et al.* 1995, Brown and Theberge 1990, Henshaw 1968, Pruitt 1979, Rominger and Oldemeyer 1990) the actual effect of snow on forage availability is poorly understood. Consequently, this element of the model remains highly speculative and is not discussed further in this thesis.

Dzus (2001) believes that in northern Alberta in most years snow conditions are not likely to affect caribou condition, birth rates or survival. Thomas (1995) discusses the effects of snow conditions on wolf predation on caribou but does not mention possible energetic consequences of snow cover on caribou foraging and access to food. Bob Wynes (pers. comm.) believes that caribou in northern Alberta are in fair to good physical condition in late winter (February), based on observation of animals captured.

2.3.8. Habitat Fragmentation and Habitat Loss

There is substantial evidence that habitat fragmentation and habitat loss

caused by forestry (Chubbs *et al.* 1993) and the oil and gas industry (Bradshaw 1994, Bradshaw *et al.* 1997; Dyer 1999, Dyer *et al.* 2001; Nellemann and Cameron 1996) affect the movements and distribution of woodland caribou. Habitat loss results from habitat fragmentation, which in northern Alberta is caused mainly by developments in oil/gas industry and forestry with consequent expansion of pipelines, well-sites, seismic lines and road networks.

2.3.8.1. The influence of habitat loss and habitat reduced use on the carrying capacity of the ecosystem

This component attempts to assess the consequences of habitat alteration by industry on the ecosystem carrying capacity for caribou. Habitat fragmentation and habitat loss reduces the amount of forage available to caribou in their habitat. If a specific amount of forage is available to caribou per unit of area in undisturbed landscape, the same unit of area of human-altered landscape will support less forage. Consequently, the carrying capacity of the system will drop. There are two ways in which habitat may be lost for caribou: 1) actual loss of habitat due to direct habitat alteration (creation of seismic lines, roads, oil wells, cutblocks); and 2) habitat loss (or degradation) due to reduced use of habitat by caribou caused by human-made structures.

1) Actual loss of habitat due to direct habitat alteration.

The amount of forage lost is calculated as follows:

Lost habitat (**LH**) is the product of the density of linear corridors (**DLC**) and the width of linear corridors (**WLC**):

$$\textbf{LH} = \textbf{DLC} * \textbf{WLC} \qquad \text{HL. 1}$$

The amount of forage lost due to direct alteration of habitat (**FL$_D$**) is the product of the amount of forage available to caribou per unit of area in undisturbed landscape (**Forage**) and the area of lost habitat (**LH**):

$$FL_D = Forage * LH \qquad\qquad HL. 2$$

Consequently, forage available per unit of area is the difference between the amount of forage available to caribou per unit of area in undisturbed landscape (**Forage**) and the amount of forage lost due to direct alteration of habitat (FL_D):

$$Forage\_Available = Forage - FL_D \qquad\qquad HL.3$$

or:

$$Forage\_Available = Forage - Forage * LH \qquad\qquad HL.4$$

or:

$$Forage\_Available = Forage - Forage * DLC * WLC \qquad\qquad HL.5$$

2) Loss of habitat due to habitat reduced use by caribou.

To calculate forage loss, I use the findings of Dyer (1999) who reports reduced use of habitat by caribou up to 96.35% in 0 -100 m buffer around roads during later winter and 62.07% in summer. In this case the lost habitat (**LH**) is replaced by area avoided (**AA**), which is the product of the density of linear corridors (**DLC**), buffer width (**BW**) and habitat reduced use (**RU**) expressed as the percent of habitat use in undisturbed landscape, modified by seasonal variations (**S**) in avoidance. Four different buffers (100 m, 250 m, 500 m, and 1000 m) are associated with roads and seismic lines, and three buffers (100 m, 500 m, 1000 m) are associated with oil wells. Habitat use may change from buffer to buffer. Therefore, for each buffer separate calculation is needed (Figure 2.7).

For linear corridors:
$$AA = DLC * BW * RU \qquad\qquad HL.6$$

For oil wells:
$$AA = OW * \pi * (BW)^2 * RU \qquad\qquad HL.7$$

Forage loss due to reduced use of habitat (FL_R) and forage available are calculated similarly as in the first case describing actual habitat alteration:

$$FL_R = Forage*AA \qquad\qquad HL.8$$

$$Forage\_Available = Forage - FL_R \qquad\qquad HL.9$$

$$Forage\_Available = Forage - Forage*AA \qquad\qquad HL.\ 10$$

Consequently, for linear corridors:

$$Forage\_Available = Forage - Forage * DLC * BW * RU \qquad HL.\ 11$$

and for oil wells:

$$Forage\_Available = Forage - Forage * OW * \pi * (BW)^2 * RU \qquad HL.\ 12$$

2.3.8.2. The influence of linear corridors on wolf predation

The purpose of this component is to simulate how linear corridors may affect
(increase or decrease) wolf predation on caribou. As REMUS is not spatial it does not
account for wolf landscape selection based on prey distribution and assumes that
wolves move in the landscape in a random fashion. This part of the model is based on
Type II functional response expressed as the number of prey eaten per predator per
unit time relative to prey density (Caughley and Sinclair 1994, Messier 1995). The
key variable in this sector of the model is predation efficiency (parameter **d** in the
equation P.14), which determines the slope of the predation rate functional response
curve in Figure 2.9. The more efficient predators are in utilizing the prey resources
the steeper is the slope of the curve, and consequently the higher predation rate at the
same given prey density. In this case, assuming that the time required to kill and eat
prey is species specific, the major constraint is the access to resources, in other words
how easy it is to find prey at its given density.

I assume that linear corridors, by changing wolf movement patterns in the
landscape influence wolves' access to prey thus changing prey encounter rate (**ER**).

The higher the encounter rate the more efficient the predators are in utilizing prey resources (Figure 2.9).

Assuming that prey encounter rate in undisturbed landscape is 1 ($ER_{UL} = 1$) and that this results in predation efficiency described by the response curve #2 in Figure 2.9, the prey encounter rate in landscape with linear corridors (ER_{LC}) may be different than the encounter rate in undisturbed landscape. If $ER_{LC} > ER_{UL}$ then, there is an increase in predation efficiency, which in turn increases predation rate at the same prey density. The $ER_{LC} < ER_{UL}$ decreases predation efficiency and gives lower predation rates at the same prey densities.

I believe that the following factors influence prey encounter rate (**ER**) in a disturbed landscape ER_{LC}:

A - relative use of linear corridors by caribou (value > 1 means that caribou select linear corridors and value <1 indicates avoidance; **A** may be season-dependent);

CM – changes in caribou mobility due to snow conditions;

DLC – the density of linear corridors;

H - human use factor;

U – relative use of linear corridors by wolves (value > 1 means that wolves select linear corridors and value <1 indicates avoidance; U may be season-dependent);

S – snow depth;

TRD – threshold road density (if the density of roads exceeds threshold level the area may become unsuitable for wolves)

TS – wolves travel speed on linear corridors;

Then,

$$ER_{LC} = ((DLC*(U/H)*(TS/S))/(A*H))*CM*S \qquad \text{LC.1}$$

The equation LC.1 is next modified by **TRD**. When the value of **TRD** is exceeded, ER_{LC} drops to zero. The flowchart for the component of the model described by the equation LC.1 is presented in Figure 2.8.

Thiel (1985) believes that the critical density of roads above which breeding wolf populations are not observed is 0.59 km/km^2. He further states that wolves are absent in areas with road densities exceeding 0.66 km/km^2. The findings of Thiel (1985) are supported by Mech *et al.* (1988). Consequently, the value of 0.66 is used for parameter **TRD** in the model. However, several authors (Mech *et al.* 1988, Thiel 1985, Thurber *et al.* 1994) point out that human use (parameter **H**) of roads may potentially alter the above numbers and determine how wolves use linear corridors. James and Stuart-Smith (2000) report that wolves may preferentially use linear corridors. As there is no quantitative data on what factors influence wolf presence on linear corridors, parameters **U** and **H** remain speculative. To estimate the values for caribou use of linear corridors (parameter **A**), the findings of Dyer (1999) are applied. According to Dyer (1999) caribou use of 0 -100 m buffer around roads during later winter is 3.65% of the expected use. This value is higher during summer (33.93%). James (1999) reports that wolves travel 2.8 times faster on corridors than in the forest. This number is used as parameter **TS** in the model.

Schneider *et al.* (2000) describe the effects of different snow conditions on caribou mobility and report that caribou movement rates decrease approximately linearly with increasing depth of snow. This linear relationship found by Schneider *et al.* (2000) is incorporated into parameter **CM,** which is the function of the maximum snow depth (**S**) that can be specified by the user in the range form 0 to 80 cm. Linking the effects on snow depth on prey encounter rate is justified by the findings of Huggard (1993), who reports that increasing snow depth decreases intervals between subsequent kills and describes this relationship by $y = 5.4 - 0.07x$, where $y -$ number of days since last kill, $x -$ snow depth.

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2.4. Model Limitations

Every simulation model has its limitations and REMUS is no exception. REMUS limitations fall into two categories: 1) design/structural limitations, and 2) lack of reliable information on specific components.

1) *Structural limitations:*

a. The model is not fully spatial. Although the model divides the landscape into two different habitat types (peatlands and uplands), it does not account for the relative distribution of patches of those habitats. REMUS does not account for animal movements either. The model is able to simulate the effects of caribou avoidance of linear corridors and oil wells on caribou fecundity and potential changes in wolf predation. However, the fact that roads act as semi-permeable barriers to caribou movements (Dyer 1999) is not reflected in the model. Similarly, wolf movements and habitat selection is not included in the model either. The fact that wolves select upland habitats is expressed in the model by wolves selecting moose as their prey species.

b. The fact that wolves can select one species as the staple prey, leads to the issue of prey switching. The model assumes that there are two values of wolf predation efficiency (parameter d), one is ten times lower than the other (by default $d_{moose} < d_{caribou}$), which results in the species with lower value of d being the selected prey. Turning the prey switching control on means that the lower value of d is assigned to the more abundant prey. In the model this change is abrupt, whereas in real situation one could expect more gradual shift.

c. At the population dynamics level, the general assumption is of no migration from and into the system from populations adjacent to the simulated one. If any of the populations in the simulation declines to zero, the species is excluded from the system and is not capable of coming back by new immigrants.

2) Lack of information:

a. Although there is evidence that black bears prey on caribou (Ballard 1994, Pitt and Jordan 1996), the information on black bear population dynamics in Alberta is scanty (Young and Ruff 1982) and the effects of black bear predation on caribou populations are poorly understood (Ballard 1994, Boileau *et al.* 1994, Ouellet *et al.* 1996). Consequently, the component of the model describing black bear predation on caribou does not account for either bear population dynamics or predator – prey interactions between caribou and bears.

b. Research on the effect of linear corridors on wolf predation on caribou is limited (James 1999, James and Stuart-Smith 2000). Some studies examined caribou habitat use and movements in relation to linear corridors (Dyer 1999, Oberg 2001). Dyer (1999) suggests that linear corridors may strongly affect habitat use by caribou. However, the reasons for the observed patterns are poorly understood. The model presents hypothetical mechanism (section 2.3.8.2) for the potential effects of linear corridors on wolf-caribou interactions. Until more information on the subject is available, this component of the model remains highly speculative.

c. Although some researchers (Adamczewski *et al.* 1988, Brown and Theberge 1990, Kelsall and Telfer 1971, Thomas 1995) point out that snow conditions may play important role in caribou population dynamics, and others report that snow cover may obstruct caribou mobility (Schneider *et al.* 2000, Stuart-Smith *et al.* 1997) there is a lack of quantitative data on the effects of different snow conditions on caribou energetics in Alberta. The model has the potential to simulate reduction in forage accessibility to caribou due to snow conditions. However, to state conclusions more information on the subject is needed.

2.5. Model Interface

The model is designed with STELLA™ Research 6.0.1 modeling software and operates in MS Windows™ environment. To run the model a user needs to install

run-time version of this software available free from High Performance Systems Inc. web site (http://www.hps-inc.com/). REMUS can be obtained from the author.

REMUS has been designed with user-friendly interface that allows easy navigation in the model, its control and outputs. The model starts with its First Screen (Figure 2.10). From this screen the user can access the description of the model, the general map of its design, the main control panel or the tutorial that familiarizes the user with the model. The control panel (Figure 2.11) allows easy navigation in the model using the right-hand side buttons, and provides its users with a possibility of manipulating the elements of the system. The model makes it possible to adjust the following components:

Natural elements of the system:
1. **The size of the total area** simulated and its habitat composition (proportion of the total area covered by lowlands);
2. **Initial density of caribou** (calves, yearlings, adults) expressed as animals/km^2. Setting the initial density of all age classes to zero is equal to complete exclusion of caribou from the system during a particular simulation;
2. **Carrying capacity for caribou forage** (kilograms of dry biomass/km^2) in lowland habitat;
3. **Wolf predation**. Here, the following elements may be controlled:
   a) **initial density of wolves** (animals/km^2). Setting the initial density to zero means total exclusion of wolves from the system during a particular simulation;
   b) **wolf territoriality** expressed as the maximum density of animals/km^2 that wolf population will not exceed due to territorial behavior (even if prey availability is high). The higher the value of wolf territoriality the higher the maximum number of wolves per pack is.
   c) **territory size** of a wolf pack;
   d) **functional response of wolves** (predation efficiency);

e) **prey selection** – by changing the values of parameters $d_{caribou}$ and d_{moose}, the user of the model can specify which species is the preferred prey;

f) **prey switching** may be turned ON or OFF;

4. **Bear predation** on caribou (proportion of calves, yearlings and adults taken by bears annually);

5. **Moose initial density** (animal/km^2). Setting the initial density to zero means total exclusion of moose from the system during a particular simulation;

6. **Carrying capacity for moose forage** (kilograms of dry biomass/km^2);

7. **Fire component** can be turned ON, or OFF;

8. **Snow conditions** (average maximum snow depth and the degree of reduced access to food resources for caribou due to snow conditions);

Anthropogenic elements of the system:

9. **Moose hunting** (proportion of adult males and females harvested annually);

10. **Caribou harvest** (proportion of calves, yearlings and adults either poached or hunted annually);

11. **The maximum density** of wolves set by wolf control;

12. **Initial density of linear corridors** (seismic lines, roads) and oil wells;

13. **Rate of change in the densities of linear corridors and oil wells**;

14. **Caribou reduced use** of 100, 250, 500 and 1000m buffers adjacent to seismic lines and roads, and 100, 500 and 1000m buffers adjacent to oil wells;

REMUS generates outputs in tabular and graphic formats. Any of the 250 variables included in the model can be graphed or tabulated. Tables allow the user to examine changes in the variables over time on monthly or yearly basis. Simulation

outputs can be automatically exported into another MS Windows based software such as MS Excel.

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TABLES

Table 2.1. Terrestrial lichens availability to caribou in different habitats. The last two measurements were done on caribou feeding sites; the first two are averages per unit of area. After Thomas and Kiliaan (1998).

Location	Habitat	Dry Biomass in kg/ha	Reference
Manitoba	Spruce/pine	870	Scotter 1965
Alberta	Pine/spruce	990	Edmonds and Bloomfield 1984
Manitoba	Spruce lowland	3170	Miller 1976
Saskatchewan	Pine/spruce	5895	Miller 1976

Table 2.2. Growth rates of lichens used by woodland caribou.

Location	Lichen species/ Habitat	Lichen growth rate	Reference
Quebec	North boreal forest, forest tundra with Black spruce as the dominant tree species. Terrestrial lichens, *Cladina* and *Cladonia spp.*	Annual increment in lichen biomass ~1%/year	Arsenault, *et al*. 1997
Newfoundland	Lichen woodland - the ecotone between the boreal forest and tundra	150 pounds per acre in subalpine range and 350 pounds per acre in lichen woodland net annual gain per hectare is 392 kg	Bergerud 1971
Norway	Different species of terrestrial lichens	20% at low biomass 10% at middle biomass 0% at maximum biomass Annual growth is a maximum of 50-70 g/m^2 at medium biomass of 500-700 g/m^2 = 5000-7000kg/ha	Gaare 1997
Finland	Terrestrial lichens on reindeer ranges	11-12% of biomass	Thomas and Kiliaan 1998

Table 2.3. Availability of plant forage in forested habitats in western North America.

Habitat	Amount of biomass (kg/ha)	Reference
Forested sites in northeastern Oregon	533 – 1783	Wickstrom *et al.* 1984
Upland aspen forest, Alberta	1381 – 1752	Renecker and Hudson 1986
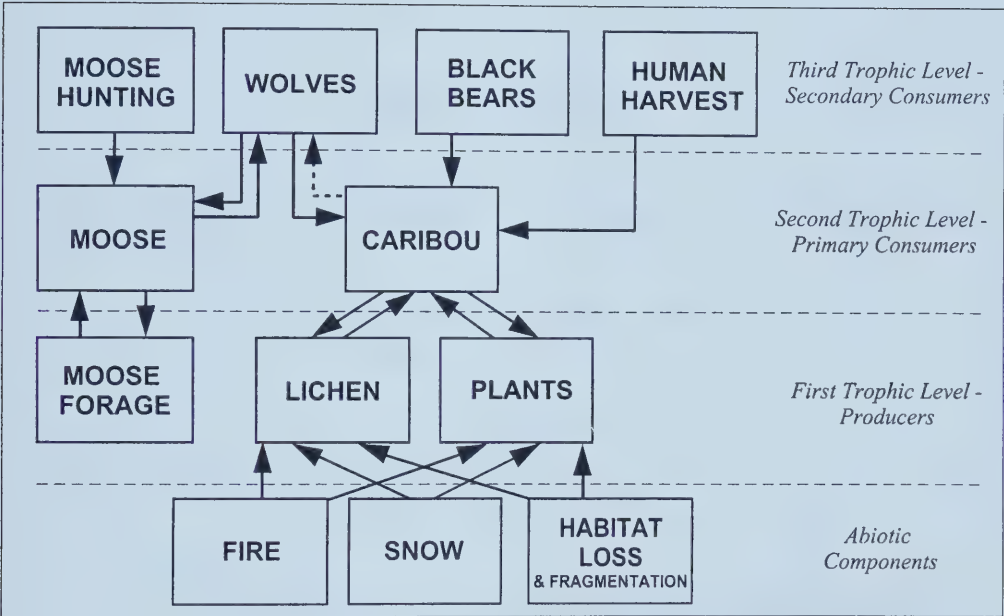
Figure 2.1. REMUS describes a three-trophic level system. The arrows indicate the relative influence of the elements of the model. The dashed arrow pointing from Caribou to Wolves reflect the caribou having relatively low impact on wolves as they constitute small proportion of wolves' diet. However, this could potentially change if the density of caribou and moose change over time.
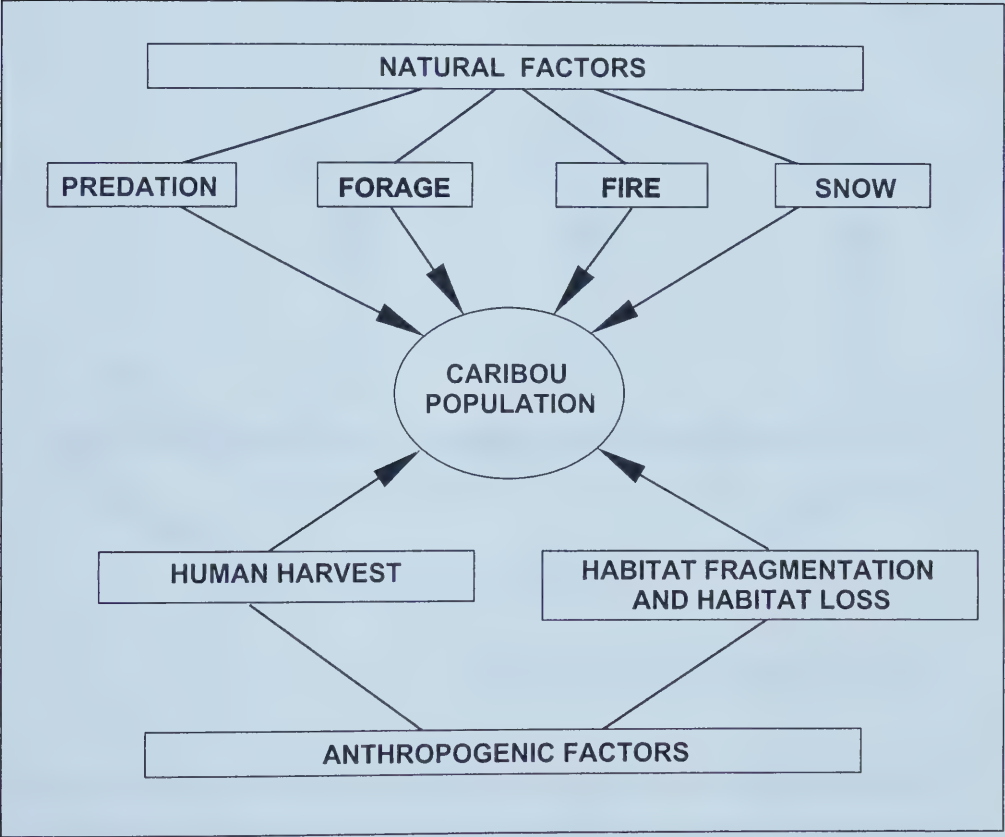
Figure 2.2. Factors influencing caribou population and included in the model. Note that this figure does not explain the relationships between the elements of the model.
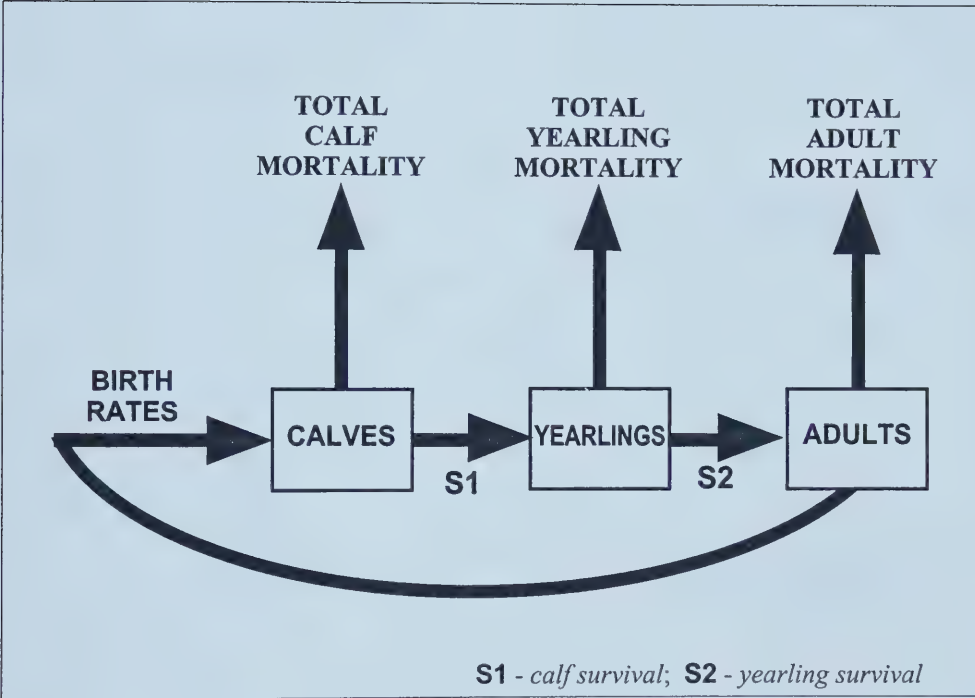
Figure 2.3. Flowchart of caribou population dynamics. The population will grow if yearling survival is greater than total adult mortality. When total adult mortality exceeds yearling survival decline is observed. Calf survival and yearling survival are equivalent to yearling recruitment and adult recruitment respectively. Total calf mortality is the sum of mortalities caused by potential food limitation, wolf and black bear predation. Total yearling and total adult mortalities are the sums of mortalities caused by potential food limitation, wolf and black bear predation, and human harvest.
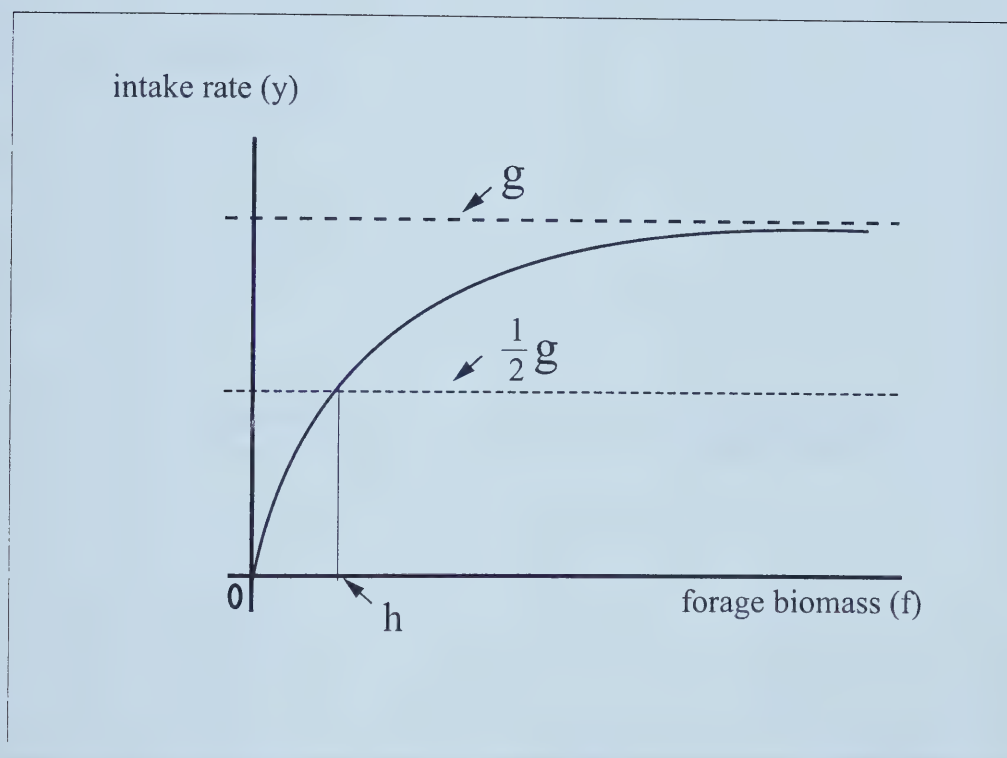
Figure 2.4. Functional response of caribou to different amounts of forage biomass. $y = f / (f + h)$; where: y – forage intake rate; f - forage available; h - foraging efficiency (the biomass of available forage at which caribou food intake rate is equal to half of the maximum intake rate); g – the maximum potential of forage intake. In the model: g = 5% of caribou body weight, h_{lichen} = 400 kg/ha, h_{plants} = 300 kg/ha, (see Section 2.3.1).
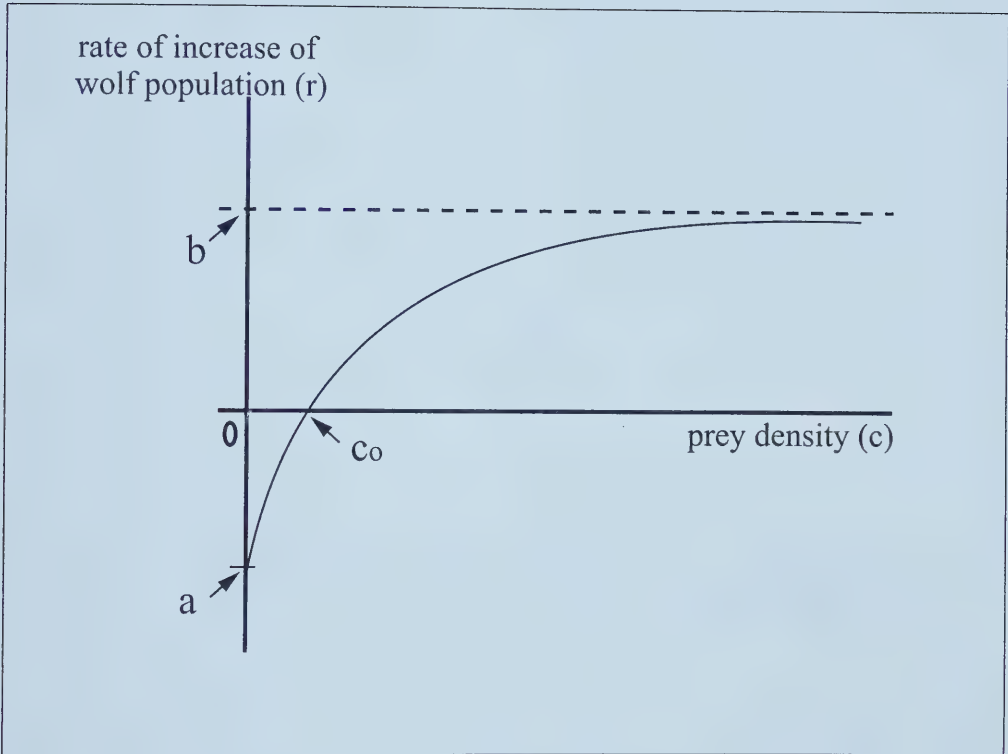
Figure 2.5. Numerical response of wolf population to prey density.

$r = a + (b * c) / (d + c)$; **a** - the maximum rate of decrease; **b** - the upper limit of "**r**" (maximum growth potential of the population given unlimited access to prey); c_0 - density of prey at which "**r**" = 0. For $c < c_0$, wolf population declines; if $c = c_0$, wolf population is stable; for $c > c_0$, wolf population increases. In the model $a_{moose} = -0.38$, $a_{caribou} = -0.112$, $b_{moose} = 1.255$, and $b_{caribou} = 0.987$, (see Section 2.3.3).
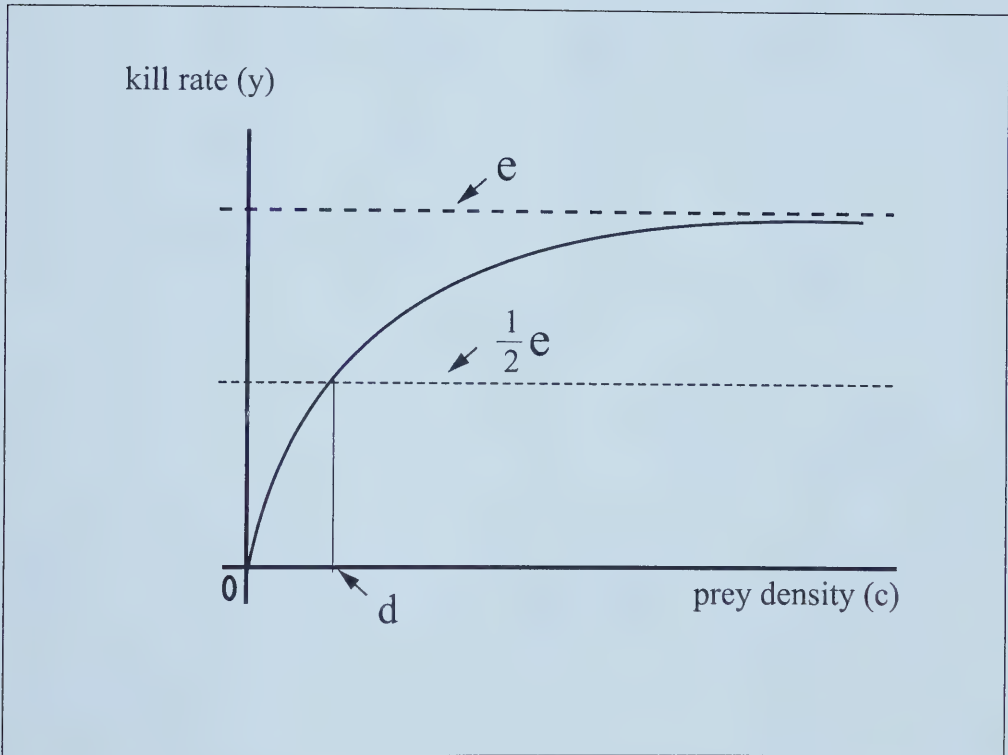
Figure 2.6. The functional response of wolf population to prey density.
$y = e * c / (d + c)$; where: y – number of prey killed per wolf per year; e – the maximum killing rate (the asymptotic killing rate when wolves are fully satiated); c – prey density; d – the prey density at half the maximum killing rate (1/2 e). In the model $d_{moose} = 0.46$, $d_{caribou} = 4.6$, $e_{moose} = 12$, and $e_{caribou} = 37$, (see Section 2.3.3).
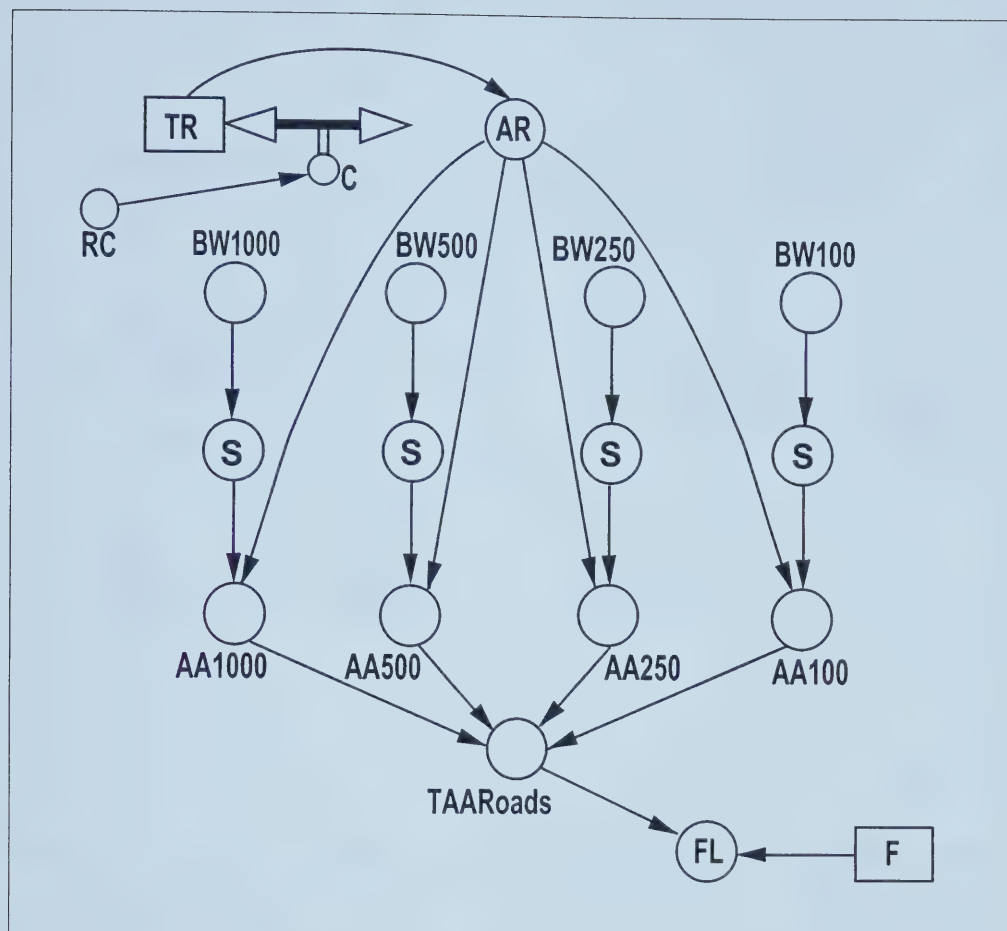
Figure 2.7. Generic model describing forage loss due to habitat reduced use by caribou. This module is adjusted for roads, seismic lines and oil wells. Symbols:

AA – area avoided

AR – total area of roads

BW – buffer width

C – change in road density

F – total amount of forage available to caribou per unit of area

FL – amount of forage lost due to avoidance

S – seasonal fluctuations in habitat avoidance

RC – rate of change in road density

TAARoads – total area avoided due to roads

TR – total density of roads
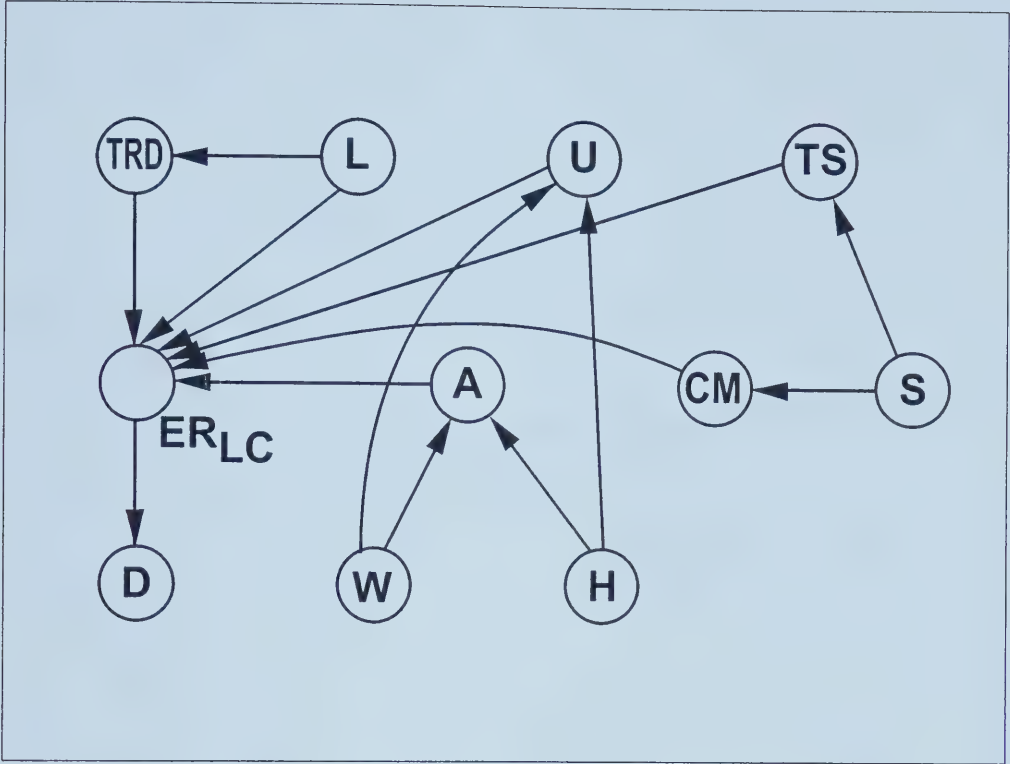
Figure 2.8. Changes in predation pressure on caribou from wolves as related to linear corridors. Symbols used:

A - relative use of linear corridors by caribou (value > 1 means that caribou select linear corridors and value <1 indicates avoidance; **A** may be season dependent)

ER_{LC} – prey encounter rate on linear corridors

CM - changes in caribou mobility due to snow conditions

H - human use factor

L – the density of linear corridors (km/km^2)

D - predation efficiency

S - snow factor

TS – wolves' travel speed on linear corridors

TRD - threshold road density

U – relative use of linear corridors by wolves (value > 1 means that wolves select linear corridors and value <1 indicates avoidance; **U** may be season dependent)

W – wolf density
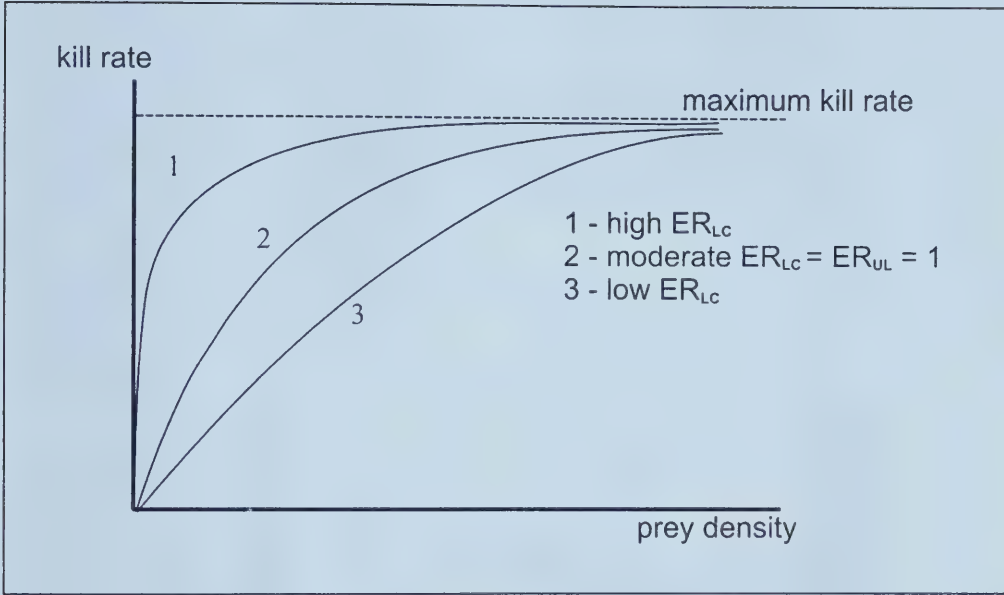
Figure 2.9. The hypothesized effect of different prey encounter rates (**ER**) on predator efficiency. **ER$_{LC}$** – prey encounter rate on linear corridors; **ER$_{UL}$** – prey encounter rate in undisturbed landscape.
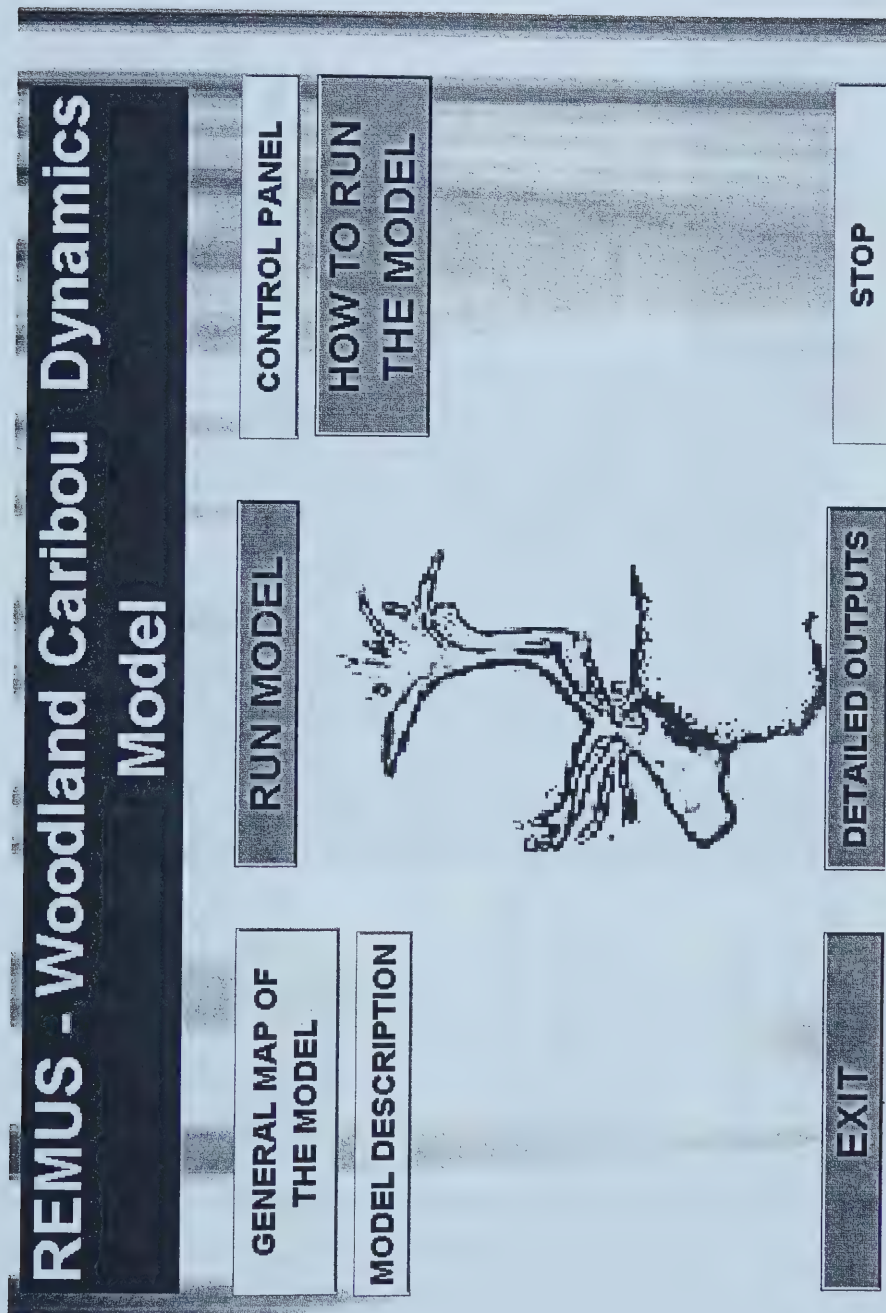
Figure 2.10. The First Screen of REMUS.
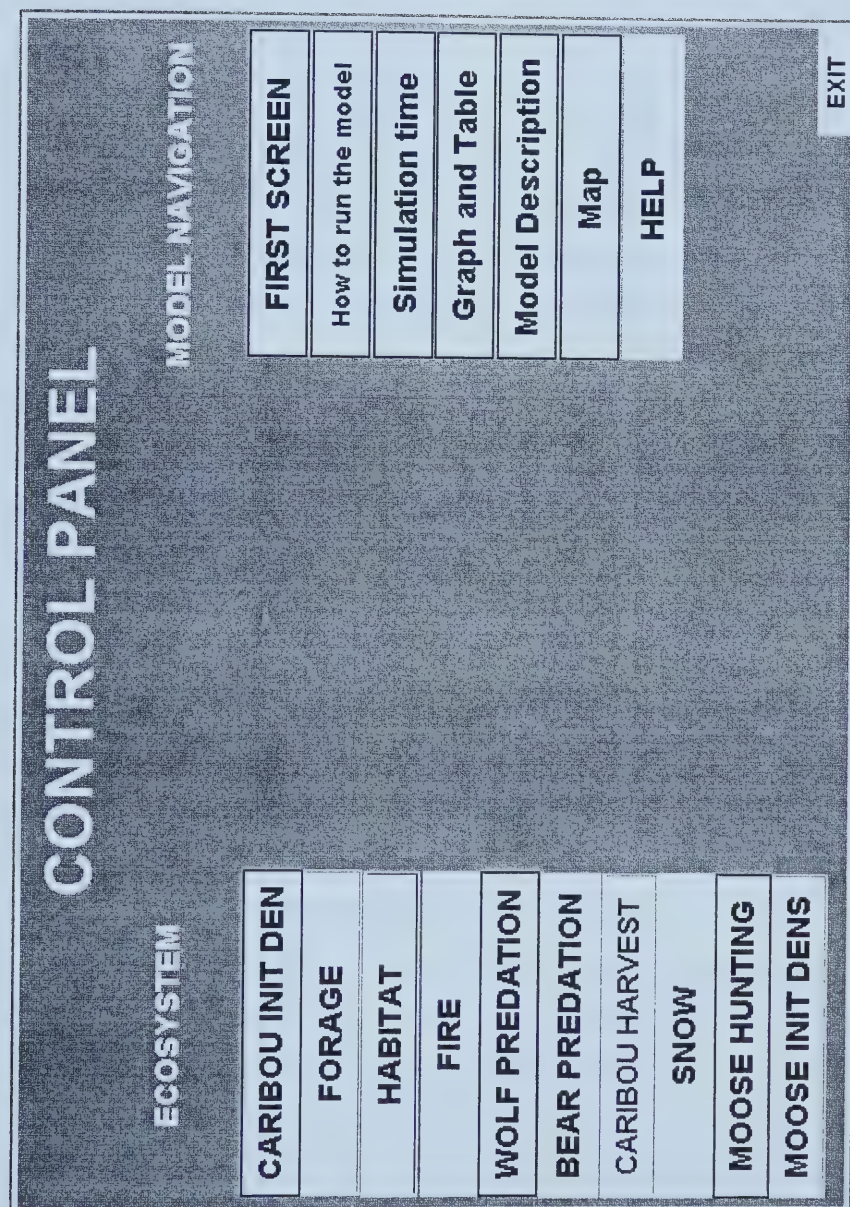
Figure 2.11. The Control Panel of REMUS.

CHAPTER III
TOP-DOWN (PREDATION) VERSUS BOTTOM-UP (HABITAT/FOOD)
CONTROL IN THE BOREAL CARIBOU SYSTEM

3.1. Introduction

Woodland caribou (*Rangifer tarandus caribou*) in Alberta exist at very low densities (Edmonds 1988, Edmonds 1991, Fuller and Keith 1981, Stuart-Smith *et al.* 1997). Bergerud (1974) argued that woodland caribou declined in the last century and recent population monitoring suggests that most caribou populations in Alberta are declining (Dzus 2001). To protect caribou populations from further decline, one needs to determine reasons for the observed decrease in caribou density, and based on this knowledge recommend mitigative strategies. Identifying the factors that result in the decline of woodland caribou is one of the central concerns of the Boreal Caribou Research Program (BCRP). My study was done as a part of a broader research initiative conducted by the BCRP.

The currently observed low density of caribou most likely results from recent declines (Dzus 2001); however, some believe that caribou exist at low densities naturally (Bergerud *et. al.* 1984, Bradshaw and Hebert 1996). Declining populations or populations that are naturally at low numbers are especially fragile, and declines can easily threaten their existence. Consequently, a good understanding of the factors that limit woodland caribou is important to ensure its long term viability. By definition, factors that determine the size of the equilibrium population are limiting factors (Caughley and Sinclair 1994). In other words, a factor is limiting a population if it has a measurable negative effect on the population's rate of change (Boutin 1992). There may be different reasons for a population to exist at low density. First, the low productivity of the ecosystem may result in its low habitat-based carrying capacity (HK) and thus limit the population's growth. Lichens that constitute the major food source for caribou (Bergerud 1972, Fuller and Keith 1981, Thomas 1995) have slow growth rates (Gaare 1997). Nevertheless, it is believed that forage resources presently are not limiting woodland caribou (Anonymous 1996, Bergerud

1996, Seip 1991), because caribou are currently at densities much lower than the carrying capacity of the ecosystem (Kansas and Brown 1992). It has been postulated that wolf (*Canis lupus*) predation limits woodland caribou populations (Bergerud 1996, Seip 1991, Seip 1992), and it is known that wolves cause most caribou mortalities (Bergerud 1988, Bergerud and Page 1987; Boreal Caribou Research Program 2000).

The first objective of my work was to test, using computer simulation, whether forage resources or predation is limiting for caribou. The second objective was to establish thresholds for forage biomass and predation that are important for caribou dynamics in the natural system.

3.2. Methods

For simulating the dynamics of caribou in response to forage resources and wolf predation, I used the computer simulation model REMUS described in Chapter 2. I simulated ideal undisturbed conditions of the boreal ecosystem by setting the human harvest and habitat loss controls to 0 (no caribou are hunted or poached, there is no human activity of any kind within the caribou range). As the size of the simulated area I used 20 000 km^2 and decided that 78% of this area was lowland habitat used by caribou (Anderson 1999, Bradshaw *et al.* 1995). This estimation was based on the description of the study area reported by James (1999). The fire component of the model was active in all simulations. This resulted in 12 to 25% of lowland habitat being unsuitable for foraging by caribou (Chapter 2). I assumed that availability of plants dropped to zero in winter and that snow did not affect caribou access to lichens. For every model settings five simulation runs were done. All simulations were done for a period of 200 years. The initial density of caribou was set to 0.07 /km^2 (Stuart-Smith *et al.* 1997) and moose to 0.25 /km^2 (Schneider and Wasel 2000). The above model settings were used in all simulation runs described in this chapter. Other controls of the model used in the simulations to test the effects of forage resources and predation on caribou dynamics were set as follows:

3.2.1. Limitation by forage

To test the argument that caribou are held at low density due to forage limitations, I excluded predation by setting the controls of the initial wolf density and black bear predation to 0. First, I assumed that the carrying capacity was 870 kg/ha and 240 kg/ha for lichens and plants respectively (Chapter 2). Next, I varied the carrying capacity of lichens to find the threshold for forage at which the caribou population stabilizes at the presently observed density.

3.2.2. Limitation by predation

To test if predation limits current caribou populations, I assumed that the carrying capacity of the ecosystem was 870 kg/ha and 240 kg/ha for lichens and plants respectively (Chapter 2), and introduced wolves by setting the initial wolf density to 0.008 /km^2 (Gunson 1992) with the upper threshold for wolf density due to their territorial behavior set to 0.059 /km^2 (Messier 1994). Next, to test the effect of wolf predation with elevated forage for caribou I increased the carrying capacity of lichens by 50% from 870 to 1305 kg /ha. Finally, I examined the dynamics of caribou under different maximum wolf densities (0.059, 0.030, 0.018, 0.008 and 0.004 /km^2) at three levels of lichen carrying capacity (1305, 870 and 730 kg / ha) to examine changes in caribou dynamics under different predation pressures and varying productivity of the ecosystem. In all simulation runs I assumed that black bears (*Ursus americanus*) were not significant predators (bear predation control set to zero).

3.3. Results

3.3.1. Limitation by forage

Outputs of the simulations showed that in the absence of predators caribou population could increase slowly from the initial density of 0.07 to 6 /km^2 in 48 years (Figure 3.1). However, the habitat-based caribou carrying capacity (HK) of the ecosystem was lower – after the increase the population declined due to overexploitation of forage. The simulations showed that in the absence of predation

the ecosystem could support caribou density stable at around 2.8 caribou /km^2 as the caribou population stabilized in the range from 2.3 to 3.4 /km^2 (Figure 3.1). This 40-fold increase from the initial caribou density indicated that caribou population at the initial density of 0.07 /km^2 was not limited by forage.

The threshold for lichen carrying capacity below which caribou population declined was 590kg/ha (Figure 3.2). Therefore, this could be the hypothetical amount of forage at which caribou population could be limited by lichen availability. For higher amounts of lichens caribou at the density of 0.07 /km^2 were not limited by forage. The model showed that if there was no predation, a 16% reduction in forage (from 870 to 730 kg/ha) could produce significant change in HK for caribou, which stabilized at around 1.8 /km^2 in the range from 1.1 to 2.2 /km^2 (Figure 3.3). This was 26-fold increase in caribou population from the initial density.

3.3.2. Limitation by predation

Introduction of wolves that could potentially increase to 0.059/km^2 into the ecosystem resulted in low amplitude stable limit cycles of caribou population around the density of 0.1 /km^2. The range was from 0.02-0.18 /km^2 and cycle period was around 40 years (Figure 3.4). Lowering the maximum potential wolf density to 0.030 /km^2 decreased slightly the amplitude of cycles to 0.05-0.13 /km^2 but did not change the pattern of caribou dynamics that fluctuated around 0.1 /km^2 (Figure 3.5). This suggested that wolf predation was limiting caribou population. The increase in the ecosystem's productivity simulated by increased carrying capacity of lichens by 50% from 870 to 1305 kg/ha resulted in higher amplitude of cycles in caribou population (from 0.02 to 1.30 /km^2) and the caribou population fluctuated around the density of 0.5 /km^2 (Figure 3.6). This was 5.6 times lower than the stable caribou density (2.8 /km^2) at 50% less forage in the ecosystem without predation (Figure 3.7). Consequently, wolf predation was still limiting caribou after a 50% increase in lichen carrying capacity. Reduction in lichen carrying capacity by 16% to 730 kg/ha resulted in complete elimination of caribou by wolves that could potentially increase to 0.030 /km^2 (Figure 3.8) due to their primary prey, moose (*Alces alces*).

Lowering the maximum potential wolf density by 60% (from 0.030 to 0.018 /km^2) stabilized caribou populations at the low density of 0.07 /km^2 (Figure 3.9). Wolf density needed to be reduced by 73% (the maximum potential wolf density 0.008 /km^2) to allow the caribou population to increase to 0.5 /km^2 (Figure 3.10). Further reduction of wolves to just 0.004 / km^2 (87% reduction of wolves) stabilized the caribou population at 1.4 /km^2 (Figure 3.11). This was 14-fold increase in caribou from the density observed when wolves could increase to 0.030 /km^2, and 2 times less than in the system without predation (Figure 3.12). This implied that even at very low densities, wolves kept caribou population below the habitat-based carrying capacity (HK) of the ecosystem. Table 3.1 and Figure 3.19 summarize the patterns of caribou dynamics in response to different forage carrying capacities (K) and varying predation.

3.4. Discussion

3.4.1. General comments

Simulation experiments showed that woodland caribou populations in Alberta apparently are not limited by habitat (assuming that the carrying capacity for lichens (terrestrial and arboreal accessible to caribou) is greater than 590 kg/ha). In contrast, model simulations revealed very strong limitation of caribou population by wolf predation. Even a 50% increase in forage carrying capacity did not release caribou from predation limitation. Similarly, significant reductions in wolf numbers did not allow caribou to reach the densities observed when wolves were not present in the system. Gunson (1992) reported that wolf density in northern Alberta was around 0.0087 /km^2. At this wolf density, caribou were still strongly limited by predation (Table 3.2, Figure 3.13). However, caribou populations increased from the initial density of 0.07 to 0.5 /km^2, a 7-fold increase. This indicated that in the natural boreal ecosystem in Alberta, with no human disturbance, caribou could coexist with wolves at densities much higher than presently observed. Consequently, based on REMUS simulations, it can be argued that factors other than predation and habitat (food resources) and the interaction of predation and habitat are responsible for the recently

observed caribou decline in Alberta. The interaction of habitat and predation shapes the population dynamics in the wolf-prey system.

3.4.2. Top-down (predation) versus bottom-up (habitat) control in the woodland caribou system in Alberta.

As REMUS gives the opportunity to examine the effects of the exclusion of a particular species, the simulated predator removal allowed studying the interactions between producers (forage for moose and caribou) and primary consumers (moose and caribou) at different levels of forage carrying capacity (K). Secondly, the inclusion of the third trophic level (predation) allowed for exploring the interactions between primary and secondary consumers.

In the simulations caribou were capable of increasing from the initial density of 0.07 to 2.8 /km^2 in the absence of wolves. Increasing the forage resources by 50% in presence of wolves resulted in caribou density 5.6 times lower (0.5 /km^2) than in the system without predation (2.8 /km^2). This suggested very strong top-down control in the caribou system.

Different theories have been proposed to address the issue of bottom-up and top-down control in ecosystems. According to the most parsimonious explanation the removal of higher trophic levels leaves lower levels intact or modified, whereas the removal of primary producers leaves no system at all (Hunter and Price 1992). REMUS is designed as a three-level trophic system (1-producers: forage for caribou and moose; 2-primary consumers: caribou and moose; 3-secondary consumers: wolves). The removal of wolves significantly modified the system by allowing ungulates to increase to high densities at which their populations were limited by food competition.

The supposition that removal of higher trophic levels can only modify the system, whereas exclusion of primary producers destroys the system, implies higher importance of bottom-up forces in ecosystems and is described by the Oksanen and

Fretwell (OF) theory (Oksanen *et al.* 1981) according to which the potential primary productivity of a region would determine the number of trophic levels it could support. In other words, in ecosystems with very low productivity, there is not enough food to sustain a second or third trophic level. However, as Bartell *et al.* (1988) pointed out that top-down and bottom-up regulation can operate simultaneously. REMUS simulations showed strong impact of the top trophic level (wolves) on lower levels, and wolf predation limited ungulate populations. This in turn resulted in much higher amounts of forage, as herbivores kept at low densities were not able to reduce food resources significantly. This strong top-down control (Figure 3.18) did not, however, change the high importance of the first trophic level. Relatively small reduction in lichen carrying capacity (by 16% from 870 to 730 kg /ha) decreased the rate of increase of caribou population and this negative change in habitat-based caribou carrying capacity (HK) caused caribou extinction (Figure 3.8) due to predation by wolves supported by the staple prey moose. This was consistent with the accepted belief that predation can cause prey extinction if there is abundant alternative prey (Bergerud and Elliot 1986, Messier 1995, Seip 1992).

In contrast to the bottom-up template for communities, the possible importance of top-down forces was stressed by Hairston *et al.* (1960) who proposed that whether or not organisms are predator or resource limited depends on their position in food chains. And, as stated by Power (1992), the relative efficacy of top-down versus bottom-up forces in food webs depends in part on the efficiency with which consumers exploit their prey. Such factors as interactions among consumers, between consumers and resources, and between distant trophic levels can influence consumer efficiency, thus modifying top-down forces in ecosystems. REMUS allows predator efficiency to be adjusted, which according to Power (1992) could affect the relative importance of top-down and bottom-up control. Future simulations in REMUS could address this important question in wildlife management.

The debate on the relative importance of top-down versus bottom-up forces continues (Herenden 1995, Huryn 1998, Moon *et al.* 1999, Power 1992, Sinclair *et al.*

2000), and is supported by field experiments (Krebs *et al.* 1995, Biggs *et al.* 2000, Sinclair *et al.* 2000). A number of models varying in complexity have addressed the issue. One of the most comprehensive set of models describing not only interactions in a series of trophic levels but also including density-dependent effects within a trophic level has been recently proposed by Sinclair *et al.* (2000). A simple model (Fretwell 1977) predicts that where food chains have odd numbers, grazers would be predator limited and landscapes should be abundant in vegetation; and where food chains have even numbers of trophic levels, plants would be grazer limited and landscapes should be barren (Fretwell 1977). The output of simulations completed in REMUS reveal strong limitation of ungulates by predation. As REMUS describes a three-level trophic system, the present work supports the idea that in systems with odd numbers of trophic levels herbivores are limited by predation.

3.4.3. Caribou population dynamics

The important question in assessing the effects of wolf predation on ungulate populations is the maximum potential wolf density that can be reached when prey is abundant but will not be exceeded due to wolves' social spacing behavior. It is known that wolves can exists at densities as high as 0.091 /km^2 (Jedrzejewska *et al.* 1996) when food resources consist of abundant prey of wild species and easily accessible livestock. Messier (1994) estimates the asymptotic value for wolf density in natural systems at 0.0587 /km^2. The simulations revealed that the uncontrolled wolf population in Alberta could potentially peak at around 0.050/km^2 (Figure 3.14) in response to prey biomass (if ungulates are not culled), and occasionally could reach the asymptotic density reported by Messier (1994). This assumed limited dispersion of wolves due to their social spacing behavior until the wolf density reached 0.059 /km^2. Setting the maximum wolf density in simulations to 0.030 /km^2 (wolves would disperse so that their density will not exceed 0.030 /km^2) suppressed the potential growth of wolf population (Figure 3.15) that could potentially increase to higher densities based on the availability of prey.

In the absence of human intervention, the upper threshold for wolf density is the product of a number of factors among which available prey biomass and wolf spacing behavior play a key role (Ballard *et al.* 1987, Fuller 1989, Gasaway *et al.* 1992, Hayes and Harestad 2000a, Messier 1985, Messier 1994, Messier 1995). The simulations have shown that what is the maximum density of wolves is very important for ungulate population dynamics. Table 3.2 describes caribou dynamics in response to different levels of predation. Caribou were cyclic if the upper threshold for wolf density was higher than 0.019 /km^2. Therefore, in the natural boreal ecosystem periodic declines in caribou caused by predation are possible if wolves can increase to high numbers. Table 3.3 shows prey equilibrium densities due to different maximum wolf densities determined by wolves social behavior. Although there was no noticeable change in prey equilibrium density (0.8 /km^2) in the range of wolf density from 0.059 to 0.018 /km^2, prey were at higher equilibrium (1.2 /km^2) at wolf density = 0.008 /km^2 and this equilibrium increased to 2 /km^2 when wolves did not exceed 0.004 /km^2. Moreover, different levels of predation resulted in different patterns of ungulate dynamics (Table 3.3). The simulations revealed that if the social behavior of wolves allows them to exist at densities higher than 0.019 /km^2: 1) stable limit cycles may be present in the natural wolf-prey system (Figures 3.14 and 3.15); 2) predation from a single predator, the wolf, suffices to cause prey declines (ungulate density was too low to cause food shortage, yet ungulate populations declined). This is contrary to Messier (1991) who stated that wolf predation could not trigger moose declines, and consistent with the findings of Boutin (1995) who reported that predation alone was capable of causing the hare (*Lepus americanus*) decline.

Messier (1994) proposed that moose would stabilize at 2 moose /km^2 in the absence of predators or at 1.3 moose /km^2 if the presence of a single predator, the wolf . He argued that these two equilibriums are created by food competition. Messier and Joly (2000) argued that if moose density exceeds some threshold, predation rate decreases with moose density and moose reach densities determined by food regulation. In REMUS simulations, food regulation only happened in the complete absence of wolf predation. At very low wolf densities the dynamics of caribou

population could be described as an 'intermediate state' between the low-density equilibrium (predator determined) and the high-density equilibrium (food determined). Here, the overall caribou dynamics is a product of predation and habitat – the shape of the population dynamics is similar to that with no predation and with low ecosystem productivity (lichen K = 730 kg /ha (Figure 3.3)) or with low predation and higher ecosystem productivity (lichen K = 830 kg /ha, and wolf density = 0.008 /km^2 (Figure 3.10)). This suggests that the balance between different levels of predation and habitat productivity (food resources) may be the ultimate factor that determines dynamics of ungulate populations.

The outputs of the simulations support the idea that a combination of habitat productivity and predation could shape caribou population dynamics (Table 3.1, Figure 3.19). The combination of lichen carrying capacity of 1305 kg/ha and low predation (0.004 wolves /km^2) produced caribou equilibrium density the same as habitat-based caribou carrying capacity (HK = 2.8 /km^2) in the system with no predation. Lichen carrying capacity set at 730 kg/ha resulted in caribou extinction if wolves were able to exist at high densities due to abundant alternative prey and wolves' social spacing behavior. When forage carrying capacity was set at 870 kg/ha caribou persisted in the system and their populations were cyclic (Figures 3.4 and 3.5). Increase in lichen carrying capacity by 50% from 870 to 1305 kg /ha produced 10-fold increase in the amplitude of caribou cycles, and 6-fold increase in caribou equilibrium density (from 0.1 to 0.6 /km^2) (Figure 3.6).

Most works dealing with regulation of ungulate populations and their dynamics (Bergerud and Snider 1988, Eberhardt and Peterson 1999, Gasaway et al. 1992, Messier 1991, Messier 1994, Thompson and Peterson 1988) attempted to assess the relative importance of habitat (food resources) and predation as potential regulatory or limiting factors, and were not concerned with the dynamic changes in the interaction of the effects of habitat and predation. Boutin (1992) pointed out that there was insufficient evidence to conclude that predation was the major limiting and/or regulatory factor for moose populations. Thompson and Peterson (1988)

believed that predation by wolves alone did not limit moose at Isle Royale. Van Ballenberghe and Ballard (1994) pointed out that whether predation is limiting or regulatory for moose populations might depend on interactions among moose, forage, weather, and hunting. I think that if future research concentrates more on examining the effects of the interaction of habitat (food) and predation, one could advance the understanding of factors that limit and regulate ungulate populations. Both habitat and predation vary in time and space. Whether predation or habitat is regulatory or limiting could depend on the dynamic interaction between the two.

3.4.4. Model validation

The ultimate test of a model is not how accurate or truthful it is, but whether it informs and improves the decision making process (Starfield 1997). However, as the goal of any model is to help to understand how the described system functions, one should try to assess the outputs of the model against the data obtained in the actual experiments. Significant research on caribou population dynamics and wolf-prey interactions has been accomplished (Bergerud and Ballard 1988, Bergerud and Elliot 1986, Bergerud and Elliott 1998, Bergerud and Snider 1988, Boertje *et al.* 1996, Boutin 1992, Dale *et al.* 1994, Gasaway *et al.* 1992, Hayes and Harestad 2000a, Hayes and Harestad 2000b, Marshal and Boutin 1999, Messier 1994, Messier and Crete 1985, Seip 1991, Seip 1992, Spaulding *et al.* 1998). Some of these findings could be used to validate my model.

Bergerud and Elliot (1986) tested the effect of wolf numbers on three caribou populations in British Columbia. They found that caribou inhabiting ranges with wolf density around 0.009-0.010 /km^2 declined. After experimental reduction of wolf numbers to 0.001-0.004 /km^2, caribou increased. These results are consistent with the outputs of REMUS simulations indicating that reducing wolves to 0.004 /km^2 should result in significant increase in caribou population. The simulations also showed that caribou could be stable even at wolf densities higher than 0.010 /km^2. Bergerud and Elliot (1986) noted caribou decline when wolf numbers were at 0.009 /km^2. There may be two reasons for this. Firstly, populations investigated by Bergerud and Elliot

(1986) most likely were exposed to bear (*Ursus spp.*) predation. To describe the effect of wolf predation on caribou, I assumed that bears were not significant predators. Secondly, the simulations suggested that high wolf predation could cause fluctuations in caribou dynamics. Consequently, it is possible that the populations examined by Bergerud and Elliot (1986) were in the decline phase. Bergerud and Elliot (1986) noted that major fluctuations in caribou numbers in British Columbia have occurred during the last century. They believed that those changes in caribou populations were caused by variations in wolf numbers.

A number of studies addressed the issue of ungulate equilibrium densities in wolf-prey systems (Bergerud and Snider 1988, Eberhardt and Peterson 1999, Gasaway *et al.* 1992, Hayes and Harestad 2000b, Messier 1994, Messier and Crete 1985, Seip 1991). Table 3.4 summarizes their findings. In most cases low- and high-density equilibria were reported. Seip (1991) noted a medium-density equilibrium (0.6 /km^2) for barren-ground caribou herds in Canada and Alaska. Seip (1991) believed that at medium-density equilibrium, caribou exhibit nutritional stress due to food competition but predation and human harvest are the limiting factors. The reported low-density equilibriums resulted from predation limitation, whereas high-density equilibriums were determined by food competition. Messier (1994) proposed two low-density equilibriums: one in the system with just one predator, the wolf (1.3 /km^2), and another with multiple predators (0.2-0.4 /km^2). Similarly, Gasaway *et al.* (1992) proposed a low-density equilibrium resulting from a combination of wolf and bear predation and high-density equilibrium in a system with one predator.

The equilibrium densities generated in REMUS simulations in response to different levels of predation are summarized in Table 3.3. Figures 3.14 – 3.17 show dynamics of the wolf-prey system in response to different maximum potential wolf densities. Prey equilibrium densities were the same (0.8 /km^2) for high wolf densities (form 0.059 to 0.018 /km^2). These could be described as low-density equilibria. At a wolf density of 0.008 /km^2 prey equilibrium density was 1.2 /km^2 (medium density equilibrium). In the system with very low wolf density (0.004 /km^2) or with no

wolves, the high-density equilibrium was found at $2 - 3.2$ prey /km^2. The fact that at constant forage carrying capacity variations in wolf numbers resulted in different equilibrium densities implied that wolf predation was limiting prey (a factor is limiting if it sets the position of the equilibrium (Van Ballenberghe and Ballard (1994)).

In the simulations, both low-density and high-density equilibriums are higher than those reported in the literature. I believe that this is due to the fact that in simulations neither predation by other predators nor human harvest were included. Moreover, the equilibrium densities generated in REMUS account for the total prey (the sum of moose and caribou densities), whereas the equilibrium densities reported in the literature (Table 3.4) do not include alternative prey species.

Although in the simulations there was no noticeable change in prey equilibrium density in the range of wolf density from 0.059 to 0.018 /km^2, prey were at medium-density equilibrium (1.2 /km^2) at wolf density 0.008 /km^2. Gunson (1992) reported that wolves in Alberta exist at density around 0.0087/km^2. It is also known that ungulate populations in Alberta exist at densities lower (Edmonds 1988, Fuller and Keith 1981, Hauge and Keith 1981, Mytton and Keith 1981, Stelfox 1993, Stuart-Smith *et al.* 1997, Schneider and Wasel 2000) than the stable equilibrium (1.2 /km^2) predicted by REMUS at wolf density equal to 0.008 /km^2. I believe this difference is due to the fact that Gunson (1992) described a system with significant human impact (both wolves and prey were culled, habitat alteration occurs in Alberta) and other potential predators (bears), factors that were not included in REMUS simulations.

Table 3.4 reveals apparent differences in the equilibrium densities reported from different studies. I believe they may be caused by a number of factors, among which differences in alternative prey species and ecosystems' productivity would seem to be most important. This stresses the importance of examining the effects of the interaction of forage and predation on the dynamics of ungulate populations. The idea of the importance of cumulative effects of different factors is also emphasized by

comparing the outputs of REMUS simulations with the threshold wolf density proposed by Bergerud (1988, 1991) needed in order to achieve stable caribou populations. Bergerud (1988, 1991) believed that caribou could coexist with wolves if wolf density did not exceed 0.0065 /km^2. Outputs of the simulations suggested that caribou could deal with wolves reaching densities as high as 0.059 /km^2. However, Bergerud (1988, 1991) referred to systems with bear predation, human harvest and industrial development, factors I did not include in the simulations.

Outputs of the simulations showed that cyclicity in caribou population dynamics could be observed if wolf numbers exceed 0.019 wolves/km^2 (Figures 3.4, 3.5 and 3.6, Table 3.1). Caribou cyclicity was caused by the dynamics of wolf-prey system in which moose were the primary prey. When the availability of prey and wolves' social behavior allowed wolves to exist at high density, these high wolf numbers triggered prey declines. Thus, in the pristine boreal ecosystem, one could expect periodic caribou declines caused by predation. Different studies investigated cyclicity in mammal populations. Boutin (1995) demonstrated that predation could cause hare declines. Krebs *et al.* (1995) concluded that three-trophic-level interaction generates hare cycles in the food-hare-predation system. Messier (1991) predicted self-perpetuating moose cyclicity in forage-moose-wolf system, and pointed out that population cyclicity seemed essential to observe moose population growth above the moose density = 0.8 /km^2 in a system with wolf predation. Peterson *et al.* (1984) suggested that populations of wolves and moose on Isle Royale could fluctuate with a period of 38 years (95 % confidence interval ±13 years), and proposed an equation for a cycle period ($t_p = 8.15M^{0.26}$, where M = body mass) to describe the dependency on body size of cycle period for birds and mammals. Using the above equation and assuming average caribou body weight 147 kg (Stelfox 1993), the cycle period would be 29.8 years. In the simulations, caribou cyclicity was due to predation. Predator-prey dynamics showed cyclicity with a period of 38 - 40 years (Figures 3.14 and 3.15), Assuming moose body weight of 434 kg (Stelfox 1993), the cycle period for the total prey (moose and caribou) would be 35.6 years, slightly less than predicted by the model but within the 95% confidence interval given by Peterson *et al.* (1984).

Seip (1991) discussed the effects of predation on caribou populations. Seip's (1991) review suggests that if predators are absent, caribou exceed density of 2.0 caribou /km^2 and can reach numbers as high as 8.9 /km^2. These differences in habitat-based carrying capacities (HK) are most likely due to variations in the productivity of the ecosystems. As predation pressure increased caribou density dropped. Seip (1991) noted that Arctic migratory herd existed at densities around $0.6 - 1.1$ /km^2. Migratory behavior resulted in spatial separation of caribou and wolves for prolonged periods during a year and this significantly decreased the effect predators could pose on caribou numbers. According to Seip (1991) the forest dwelling caribou populations existed at lowest densities (0.03 /km^2) as the impact of predation on those populations was highest due to predators being present in caribou range year-round and the abundance of wolves' primary prey (commonly moose).

Outputs of the simulations were consistent with Seip's (1991) review. REMUS predicts that in the absence of predators unhunted woodland caribou in Alberta can exist at density as high as 2.8 /km^2 (Table 3.1, Figure 3.1). As predation increases, caribou numbers decrease. If wolves are uncontrolled, REMUS predicts caribou density to be around 0.1 /km^2 in pristine caribou habitat (given that moose is the primary and preferred prey).

Caribou population dynamics generated by REMUS were similar to the outputs of the model proposed by Messier *et al.* (1988) for the George River Caribou Herd. Messier *et al.* (1988) proposed four different hypothetical scenarios of caribou population dynamics resulting from four different rates of increase and suggested that decreasing the rate of increase by hunting may prevent overshooting of the carrying capacity (HK) followed by a dramatic decline. Consequently, by adjusting hunting, one could smooth the dynamics of the herds. REMUS simulations suggested that the rate of caribou increase (and potential overshooting of HK) might be determined by forage availability, predation and the combination of the two. Thus, knowing the forage carrying capacity of the ecosystem, by manipulating the density of predators

one should be able to achieve the desired dynamics of the caribou population (Figures 3.20 and 3.21).

3.5. Conclusions and Management Implications

REMUS simulations lead to following conclusions and management recommendations:

3.5.1. Conclusions

1) The potential of woodland caribou habitat in the boreal ecosystem in Alberta is high - if there is no predation, in natural conditions the area can support 2.8 caribou /km^2.

2) In the absence of human impacts, caribou can deal with high predation. Even with uncontrolled wolf populations, caribou can exist at densities around 0.1 /km^2.

3) To release predation pressure on caribou in a natural undisturbed ecosystem, significant reductions in wolf numbers are needed (wolf density needs to be lowered to at least 0.004 /km^2).

4) Wolf predation limits caribou, but caribou can coexist with wolves at densities (both wolves and caribou) higher than presently observed.

5) Works dealing with wolf-prey equilibrium and regulation and/or limitation of ungulate populations by predation underestimate the effects of the interaction of habitat (forage resources and habitat productivity) and predation on equilibrium density of ungulates.

6) The model reveals that food competition is not necessary to trigger declines in ungulate dynamics. According to REMUS simulations, predation alone can precipitate prey declines.

7) The model needs to be made fully spatial to simulate the effects of spatial separation hypothesis (James 1999) and dispersion at low density hypothesis (Bergerud *et. al.* 1984). In the model I simulated the spatial separation hypothesis by assigning different prey selectivity for moose and caribou (moose were selected by wolves preying 10 times more efficient on moose than caribou). Also, I did not include any mechanisms accounting for caribou behavior to disperse at low density to

decrease predation. I assumed that there was no difference in moose and caribou social behavior.

3.5.2. Management and Research Implications

1) Simulations illustrated that cycles in a natural wolf-prey system are possible and the period of cycles is around 40 years. If cycles are present, decline (followed by increase) in caribou may be due to predation. To validate this statement long-term population monitoring of wolves and their prey is needed.

2) It is important to measure how wolf density changes in relation to prey availability (biomass). Understanding the mechanism of wolf social spacing behavior is crucial to assess the effects of wolf predation on caribou dynamics as wolf density has a strong effect on prey dynamics.

3) Simulations revealed strong top-down control in the caribou system. To increase caribou numbers predators need to be controlled and very significant reductions (to 0.004 wolves /km^2) are necessary. It should be stressed that this applies to the natural system with no human impact only. At present, the boreal ecosystem in Alberta is modified by human activities and wolf control may not increase caribou numbers. The issue of wolf control in relation to human impact on caribou habitat is addressed in Chapter 4 of this thesis. Moreover, the simulations have clearly shown that caribou are able to persist in the ecosystem with high wolf predation, at densities higher than presently observed.

4) To recommend mitigation in caribou conservation one needs to know the potential of habitat in the boreal ecosystem in Alberta to support caribou (what is the habitat-based caribou carrying capacity). To assess carrying capacity, research on forage biomass in caribou habitat is needed. Carrying capacity affects the ability of caribou to deal with predation and thus has important implications for the effects of industry on predator-prey dynamics and potential wolf control.

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TABLES

Table 3.1. Caribou population densities and changes in caribou densities in relation to the initial density of 0.07 caribou /km^2 resulting from different levels of lichen carrying capacity (K) and varying wolf predation. Numbers in brackets in predation column indicate the maximum potential wolf density (wolf /km^2); numbers in brackets in caribou density column indicate amplitude of cycles if present.

Predation	Lichen K (kg/ha)	Caribou density (animal/km^2)	Change relative to 0.07 /km^2 density
NO	870	2.80	40.0 fold increase
NO	730	1.80	26.0 fold increase
NO	590	0.07	No change
YES **(0.030)**	1305	(0.02-1.30) 0.50	7.0 fold increase
YES **(0.030)**	870	(0.05-0.13) 0.10	1.4 fold increase
YES **(0.030)**	730	0.00	Extinction
YES (0.059)	870	(0.02-0.18) 0.10	1.4 fold increase
YES (0.030)	870	(0.05-0.13) 0.10	1.4 fold increase
YES (0.018)	870	0.07	No change
YES (0.008)	870	0.50	7.0 fold increase
YES (0.004)	870	1.40	20.0 fold increase
YES (0.059)	730	0.00	Extinction
YES (0.030)	730	0.00	Extinction
YES (0.018)	730	0.00	Extinction
YES (0.008)	730	0.00	Extinction
YES (0.004)	730	0.07	No change
YES (0.059)	1305	(0.01-1.60) 0.60	8.5 fold increase
YES (0.030)	1305	(0.02-1.30) 0.50	7.0 fold increase
YES (0.018)	1305	1.80	25.0 fold increase
YES (0.008)	1305	2.60	37.0 fold increase
YES (0.004)	1305	2.80	40.0 fold increase

Table 3.2. Caribou population dynamics in response to different levels of predation determined by wolves' social behavior. The third column illustrates the change in caribou density in relation to habitat-based caribou carrying capacity (HK = 2.8 /km^2) in the system with no predation and lichen K = 870 kg/ha (see Figure 3.1). Numbers in brackets in the caribou density column indicate the amplitude of stable limit cycles if present.

Maximum potential wolf density (animal /km^2)	Caribou density (animal /km^2)	Change relative to HK = 2.8 /km^2
0.059	(0.02-0.18) 0.1	28.0 fold decrease
0.030	(0.05-0.13) 0.1	28.0 fold decrease
0.018	0.07	40.0 fold decrease
0.008	0.50	5.6 fold decrease
0.004	1.40	2.0 fold decrease

Table 3.3. Prey equilibrium densities and patterns of prey dynamics at different levels of predation determined by wolves' social behavior. Prey is the sum of moose and caribou densities.

Wolf maximum potential density (animal / km^2)	Prey equilibrium density (animal / km^2)	Pattern of prey dynamics
0.059	0.8	Stable limit cycles (0.1-1.5 /km^2)
0.030	0.8	Stable limit cycles (0.2-1.2 /km^2)
0.018	0.8	Stable equilibrium
0.008	1.2	Stable equilibrium
0.004	2.0	Stable equilibrium
0.000	3.2	Stable equilibrium

Table 3.4. Reported prey equilibrium densities resulting from different pressures of predation.

Prey equilibrium density (animals /km^2)			Prey species	Reference
Low	Medium	High		
0.4		2 - 4	Moose	Messier and Crete 1985
0.07 - 0.12			Moose	Hayes and Harestad 2000b
0.045 - 0.4		1.45	Moose	Gasaway *et al.* 1992
0.4		2 - 3	Moose	Bergerud and Snider 1988
1.3 or 0.2 - 0.4		2	Moose	Messier 1994
	0.6		Caribou	Seip 1991
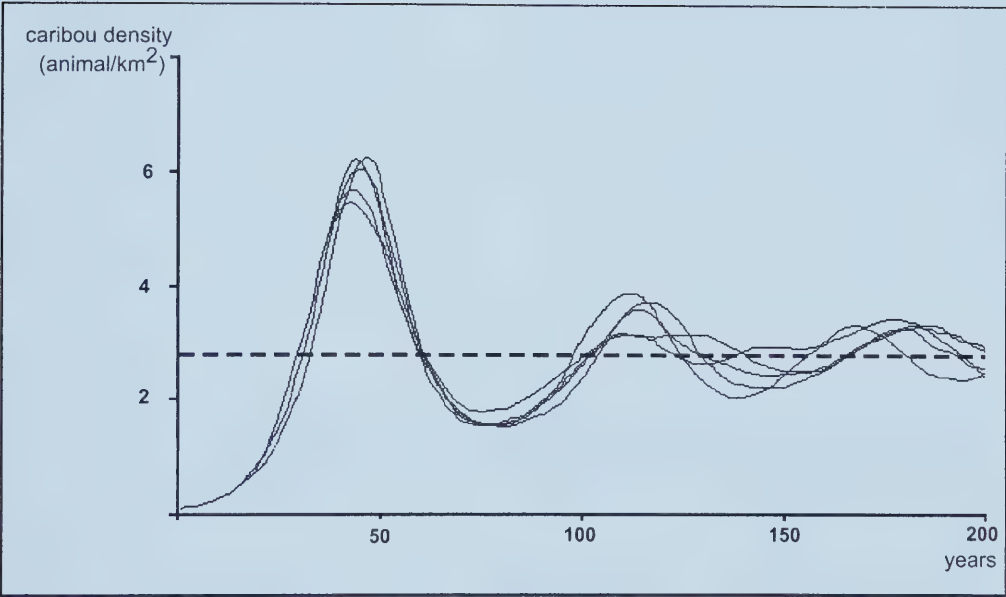
Figure 3.1. Caribou population dynamics in the absence of predation and with lichen carrying capacity equal to 870 kg/ha. Initial caribou density 0.07 /km². The dashed line represents habitat-based caribou carrying capacity (HK = 2.8 /km²). Each line represents a simulation run.
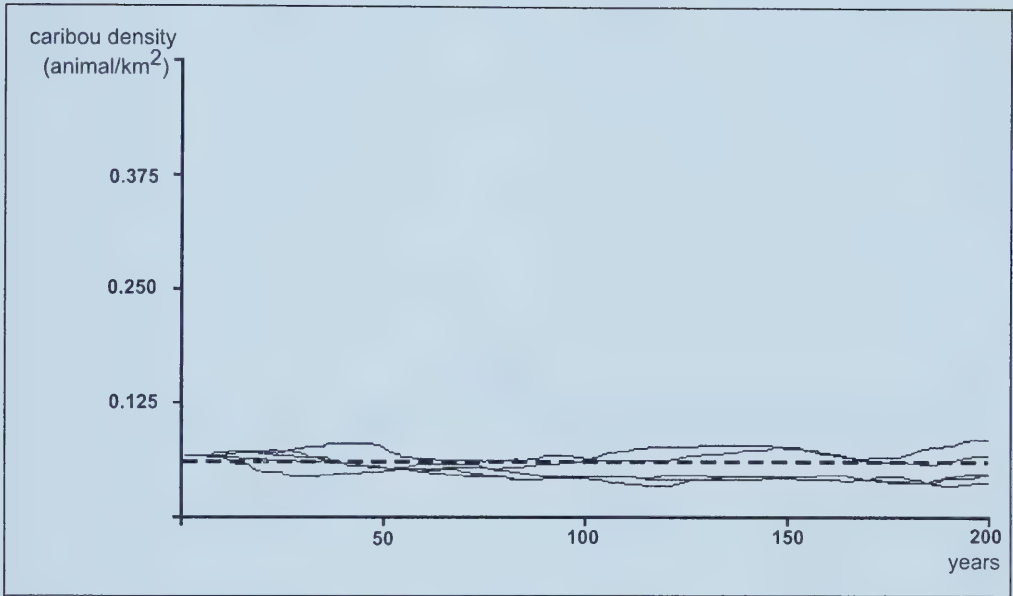
Figure 3.2. Caribou population dynamics in the absence of predation and with lichen carrying capacity equal to 590 kg/ha. Initial caribou density 0.07 /km^2. The dashed line indicates habitat-based caribou carrying capacity (HK = 0.07 km^2). Each line represents a simulation run.
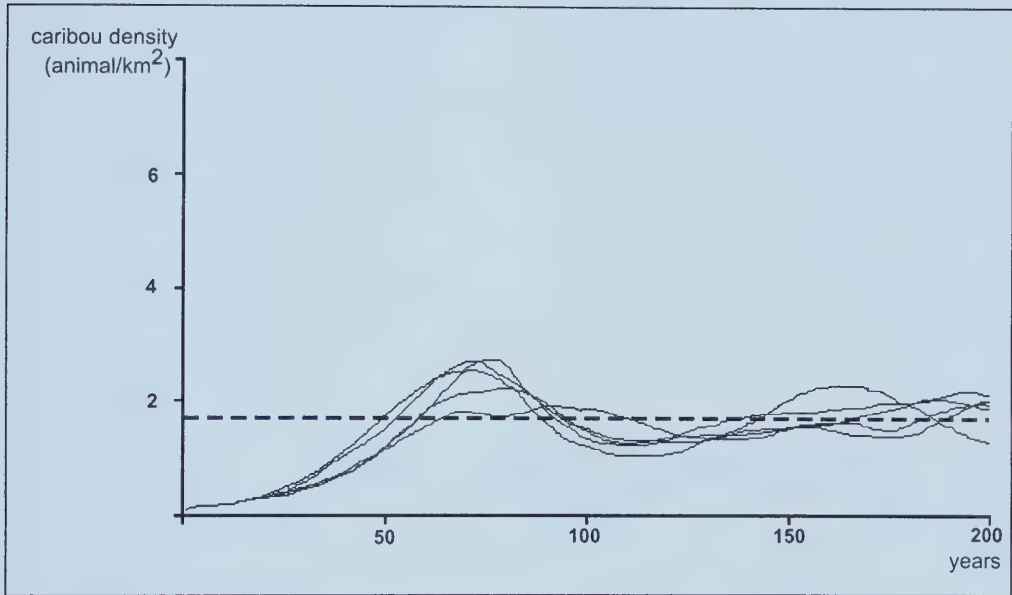
Figure 3.3. Caribou population dynamics in the absence of predation and with lichen carrying capacity (K) = 730 kg/ha. Initial caribou density = 0.07 /km^2. The dashed line indicates habitat-based caribou carrying capacity (HK = 1.8 /km^2). Each line represents a simulation run.
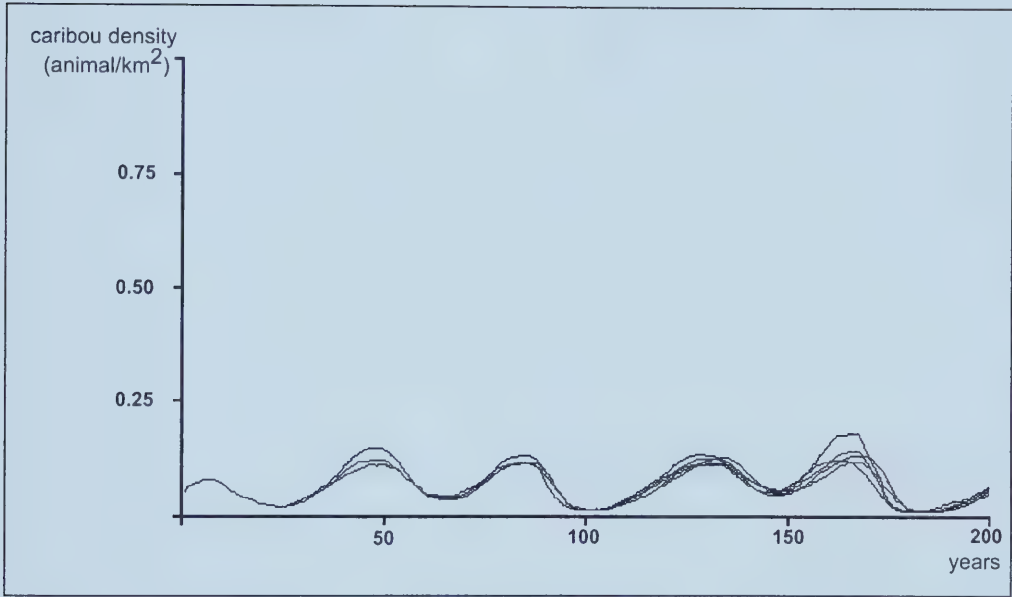
Figure 3.4. Caribou population dynamics when wolves could increase to the maximum density of 0.059 /km², and with lichen carrying capacity (K) = 870 kg/ha. Initial caribou density = 0.07 /km². Each line represents a simulation run.
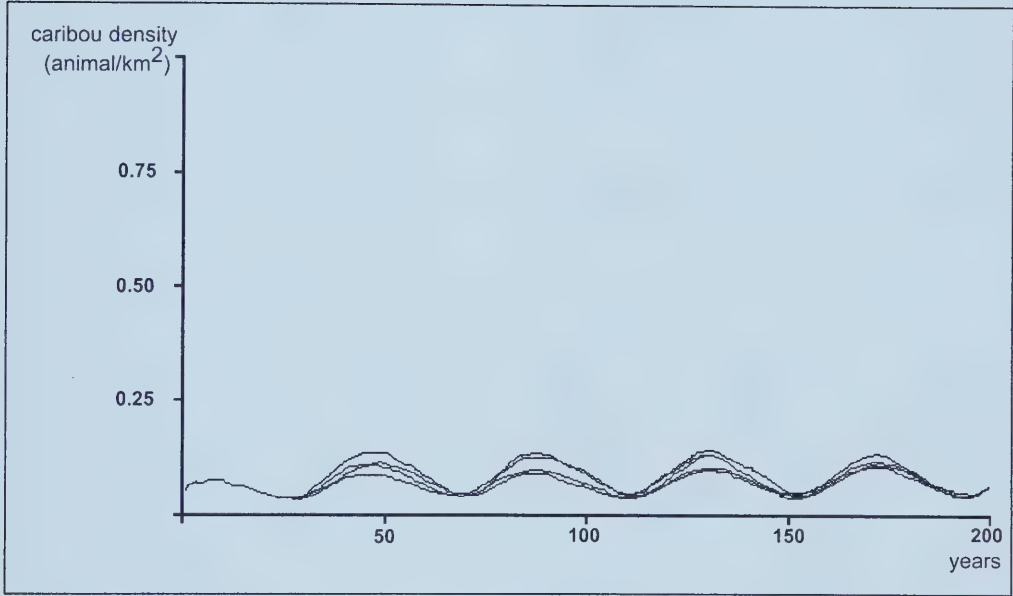
Figure 3.5. Caribou population dynamics when wolves could increase to the maximum density of 0.030 /km^2, and with lichen carrying capacity (K) = 870 kg/ha. Each line represents a simulation run.
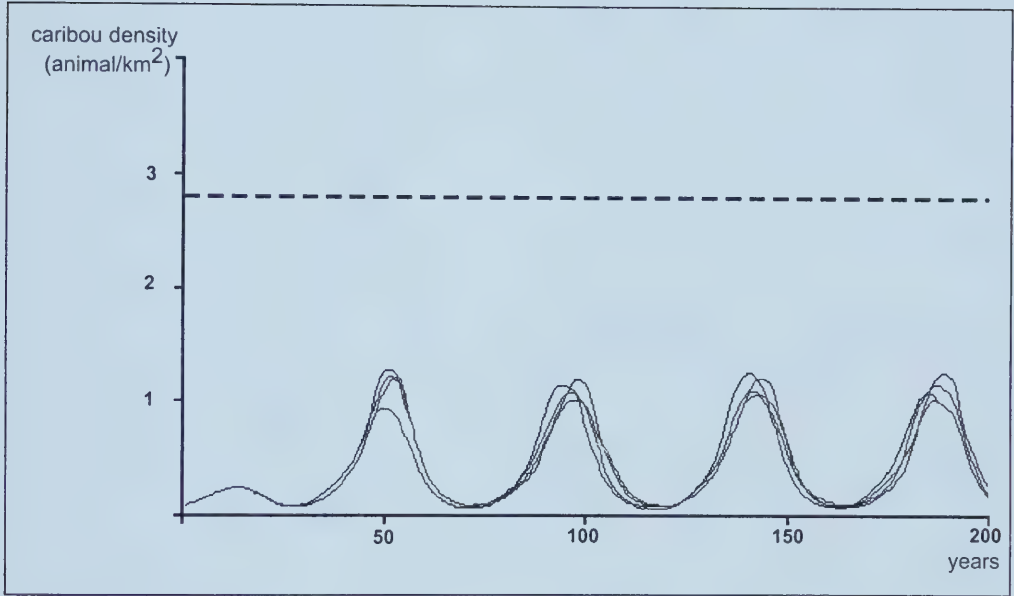
Figure 3.6. Caribou population dynamics with the maximum potential wolf density = 0.030 /km^2 and increased carrying capacity of lichens (K) by 50% (from 870 to 1305 kg/ha). The dashed line indicates habitat-based caribou carrying capacity (HK) in the system with no predation and lichen K = 870 kg/ha (see Figure 3.1). Initial caribou density 0.07 /km^2. Each line represents a simulation run.
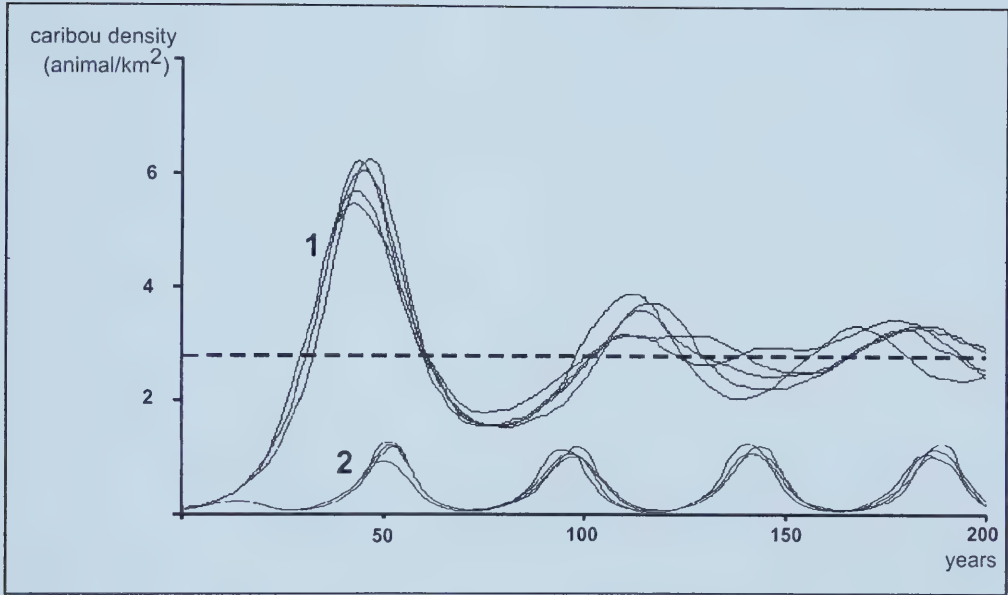
Figure 3.7. Initial caribou density = 0.07 /km². **1** – Caribou population dynamics in the system with no predation and lichen carrying capacity (K) = 870 kg/ha; **2** – Caribou population dynamics with predation and increased lichen carrying capacity (K) by 50% (from 870 to 1305 kg/ha). The dashed line indicates habitat-based caribou carrying capacity (HK) in the system with no predation and lichen K = 870 kg/ha (see Figure 3.1). Each line represents a simulation run.
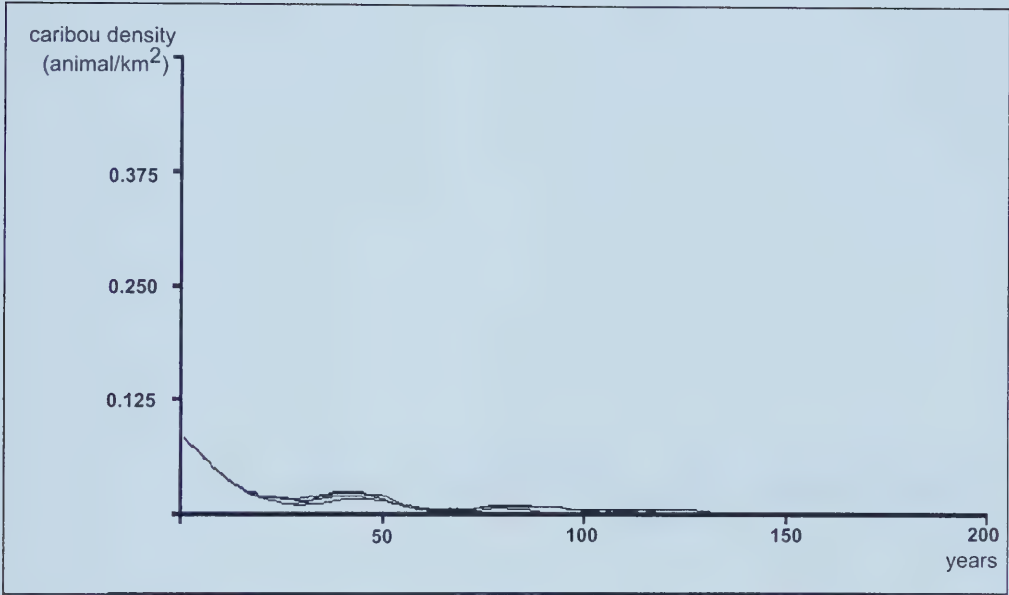
Figure 3.8. Caribou population dynamics under reduced lichen carrying capacity (K) by 16% (from 870 to 730 kg/ha) and with predation present (the maximum potential wolf density = 0.030 /km^2). Initial caribou density = 0.07 /km^2. Each line represents a simulation run.
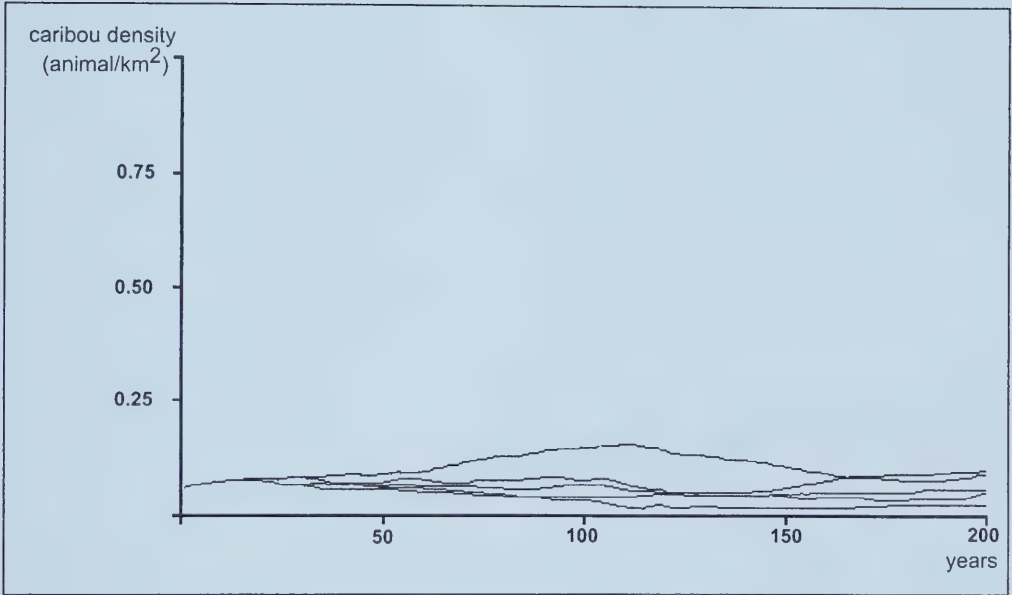
Figure 3.9. Caribou population dynamics after lowering the maximum potential wolf density by 60% (from 0.030 to 0.018 /km^2). Lichen carrying capacity (K) = 870 kg/ha, and caribou initial density = 0.07 /km^2. Each line represents a simulation run.
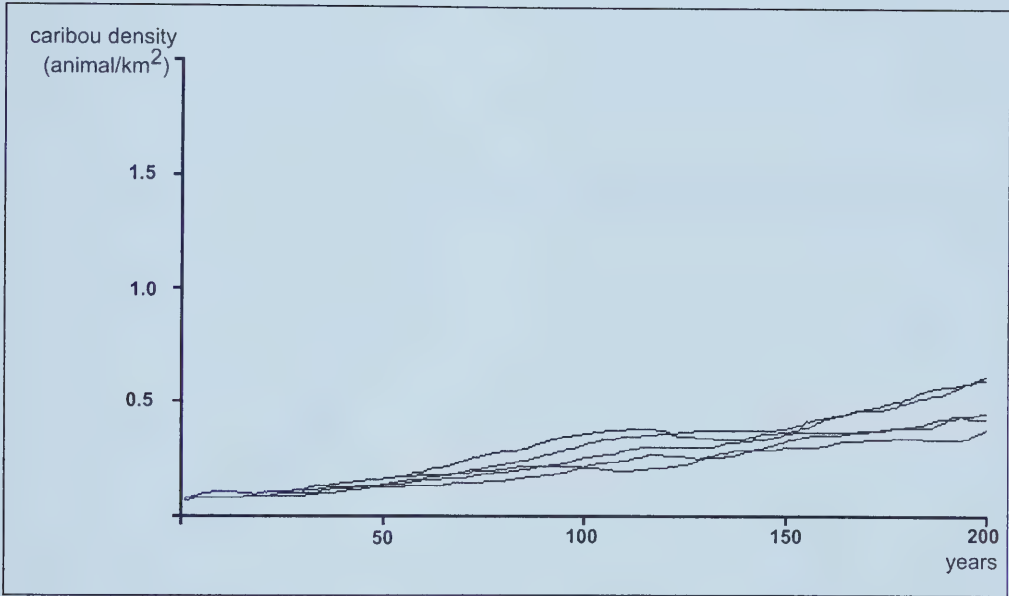
Figure 3.10. Caribou population dynamics when the maximum potential wolf density was reduced by 73% (from 0.030 to 0.008 /km^2) and with lichen carrying capacity (K) = 870 kg/ha. Each line represents a simulation run.
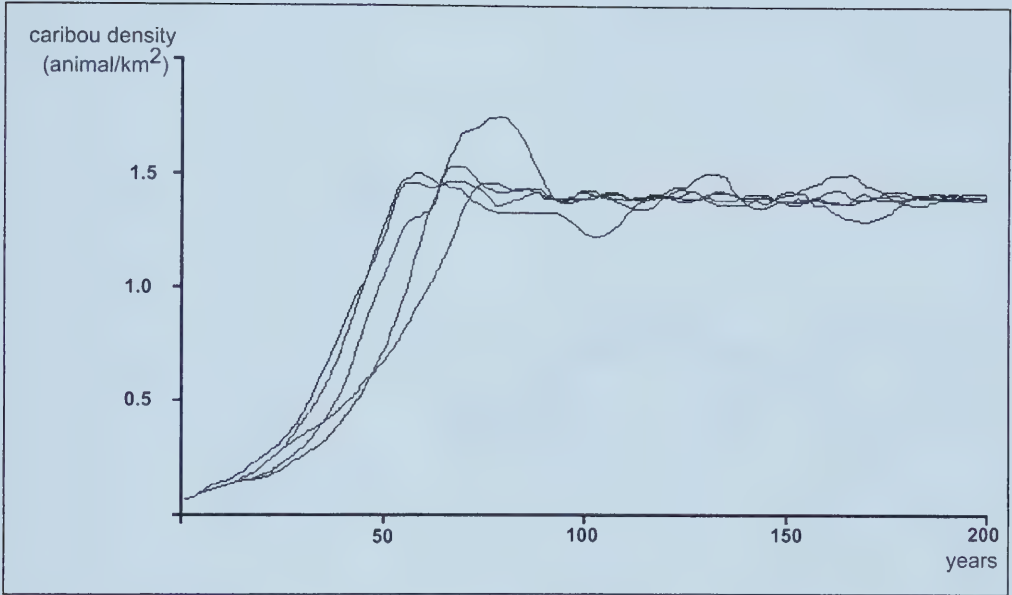
Figure 3.11. Caribou population dynamics when the maximum potential wolf density was reduced to 0.004 / km^2 (87% reduction from 0.030 /km^2) and lichen carrying capacity (K) = 870 kg/ha. Initial caribou density 0.07 /km^2. Each line represents a simulation run.
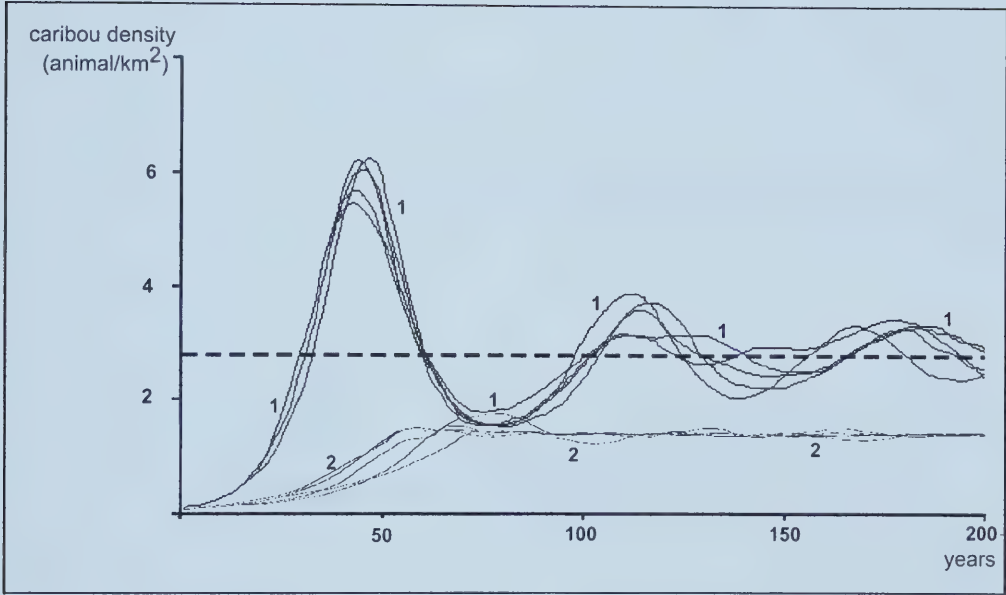
Figure 3.12. Caribou population dynamics at lichen carrying capacity (K) = 870 kg/ha. **1** – no predation; **2** – the maximum potential wolf density = 0.004 /km^2. The dashed line indicates habitat-based caribou carrying capacity (HK) in the system with no predation. Caribou initial density is 0.07 /km^2. Each line represents a simulation run.
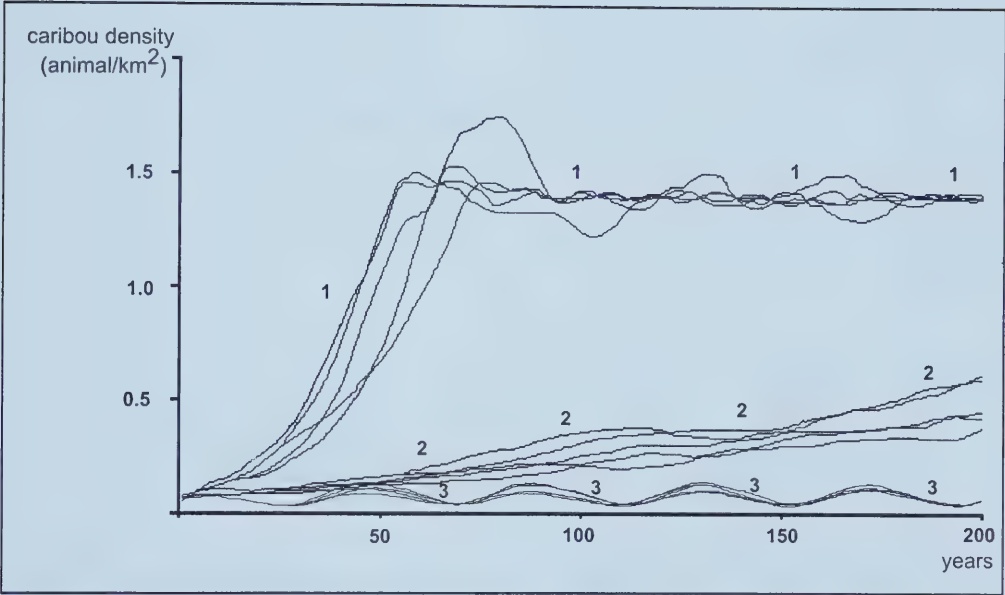
Figure 3.13. Caribou population dynamics at constant level of forage carrying capacity (K) = 870 kg/ha, and different levels of maximum densities of wolves: **1** - 0.004, **2** - 0.008, and **3** – 0.030 wolves /km². Caribou initial density is 0.07 /km². Each line represents a simulation run.
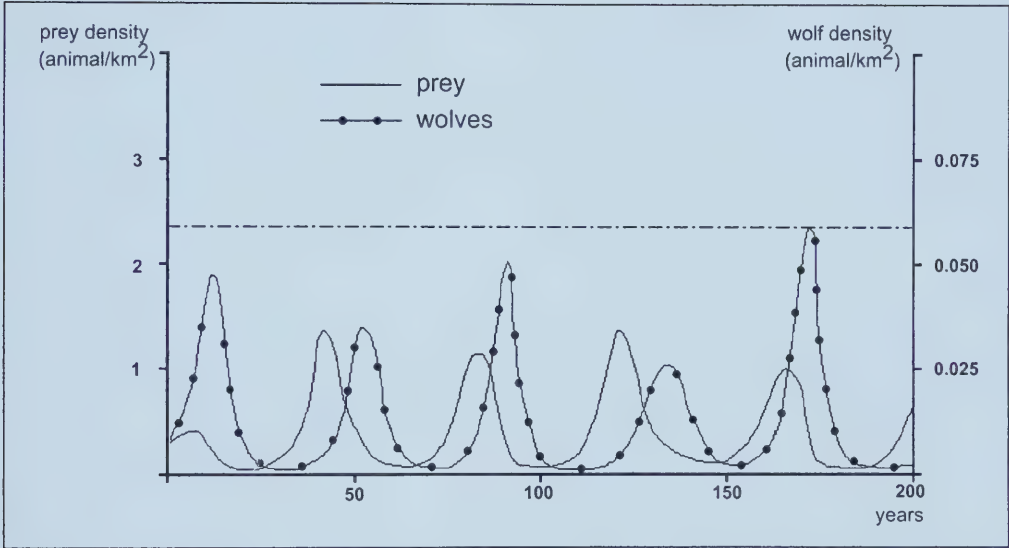
Figure 3.14. Predator and prey dynamics when wolves could increase to the maximum density of 0.059 /km^2 (dashed line). Prey is the sum of moose and caribou.
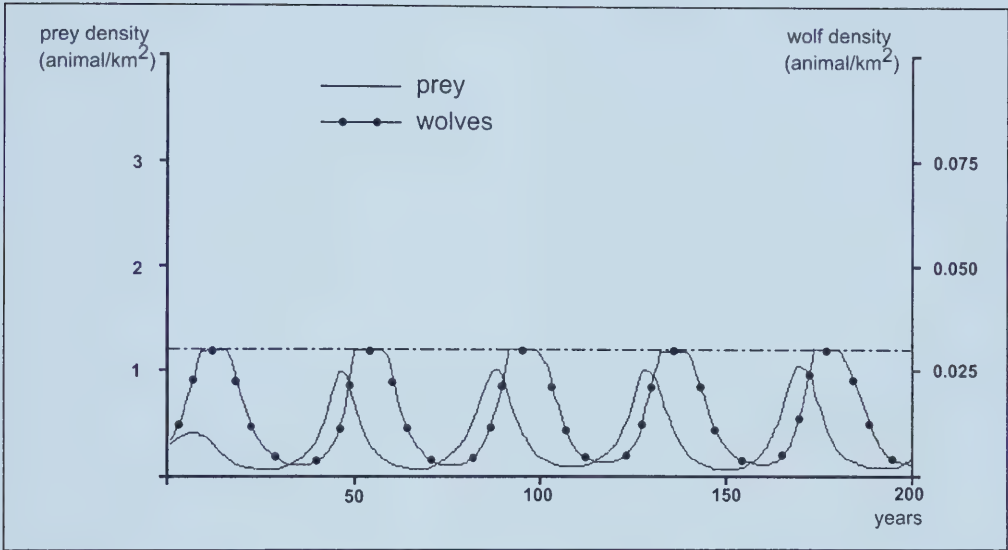
Figure 3.15. Predator and prey dynamics when wolves could increase to maximum density of 0.030 /km^2 (dashed line). Prey is the sum of moose and caribou.
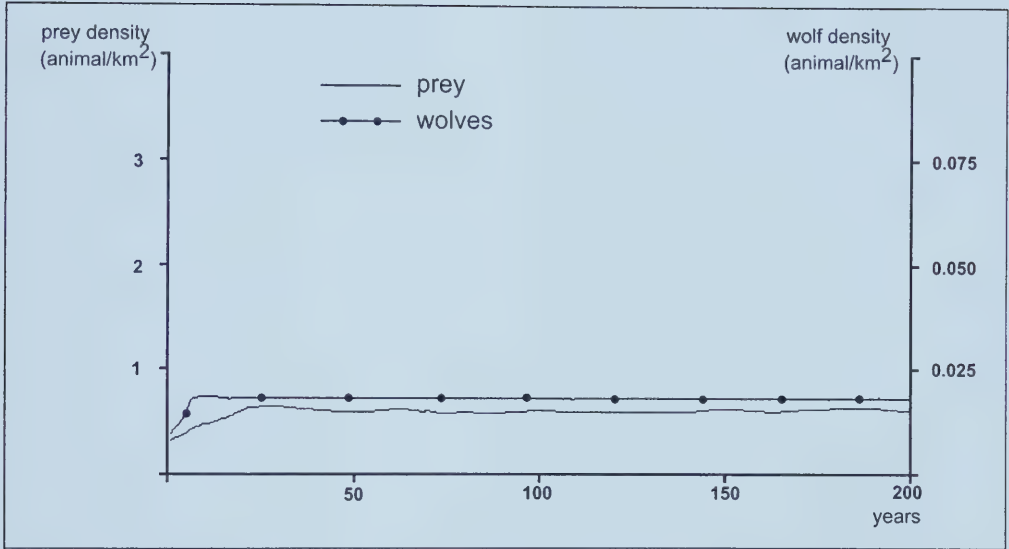
Figure 3.16. Predator and prey dynamics when wolves could increase to maximum density of 0.018 /km^2. Prey is the sum of moose and caribou.
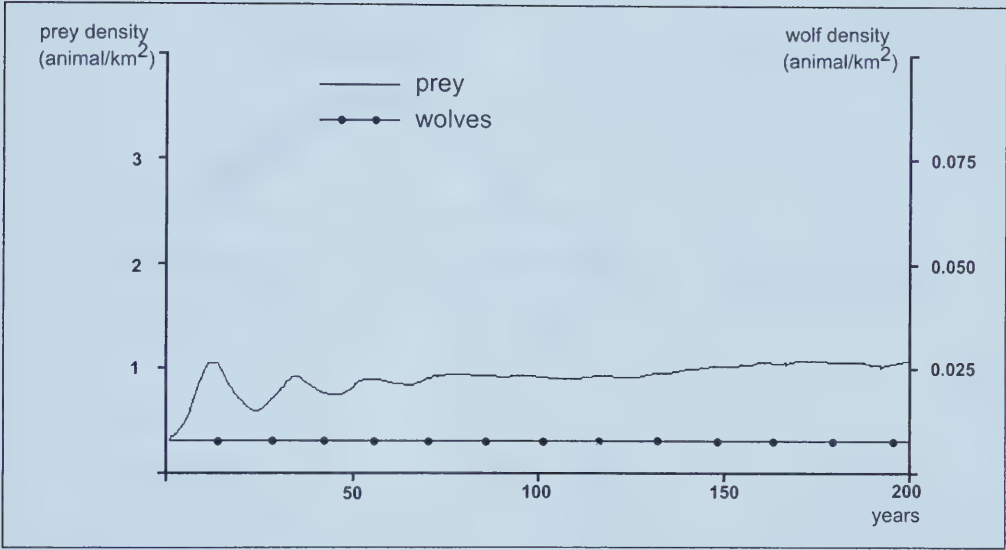
Figure 3.17. Predator and prey dynamics when wolves could increase to maximum density of 0.008 /km^2. Prey is the sum of moose and caribou.
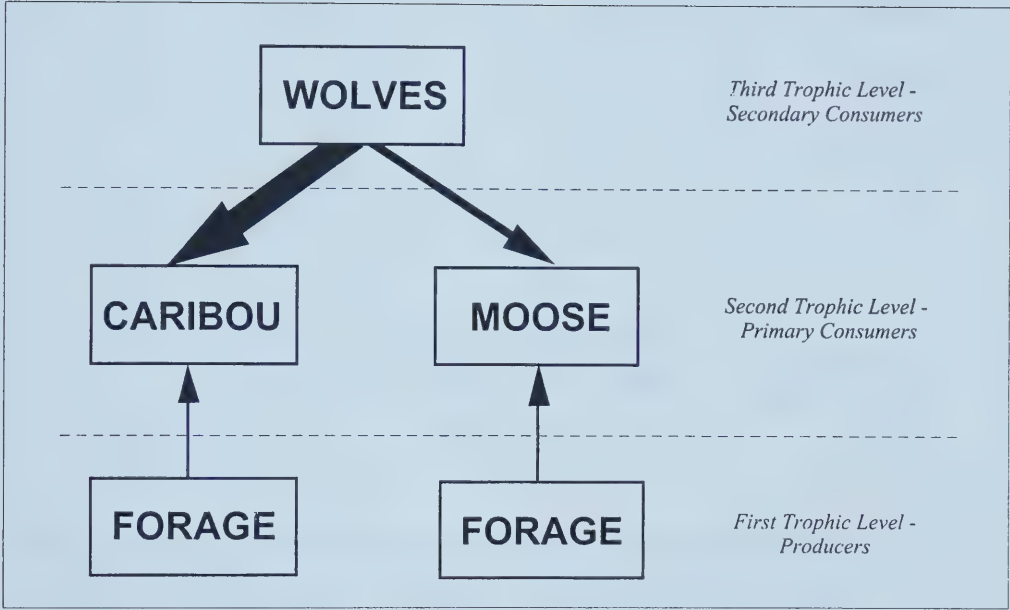
Figure 3.18. REMUS simulations showed strong top-down control in the moose/caribou – wolves system. Arrows and their relative thickness indicate what elements of the system have stronger influence in each branch (e.g., moose are the primary prey for wolves, and wolves have stronger effect on moose population than forage). The arrow indicating wolves' influence on caribou is thicker than the corresponding wolf-moose arrow to show that the impact of wolves is stronger on caribou than moose (wolves are able to cause caribou extinction if ecosystem productivity is reduced).
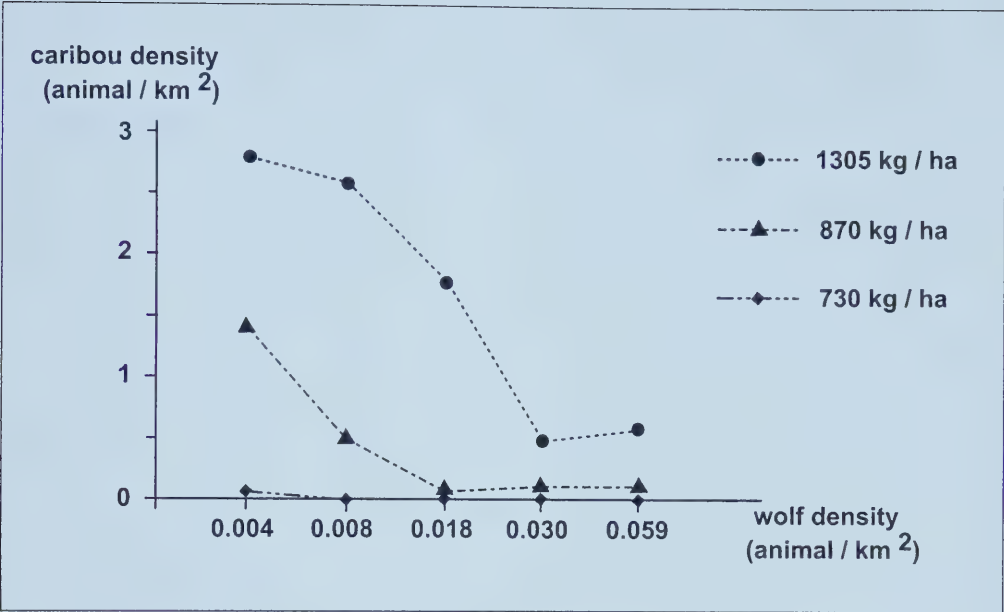
Figure 3.19. Caribou equilibrium densities resulting from 3 different lichen carrying capacities (K = 730, 870 and 1305 kg /ha) and 5 different wolf densities (0.004, 0.008, 0.018, 0.030 and 0.059 / km^2).
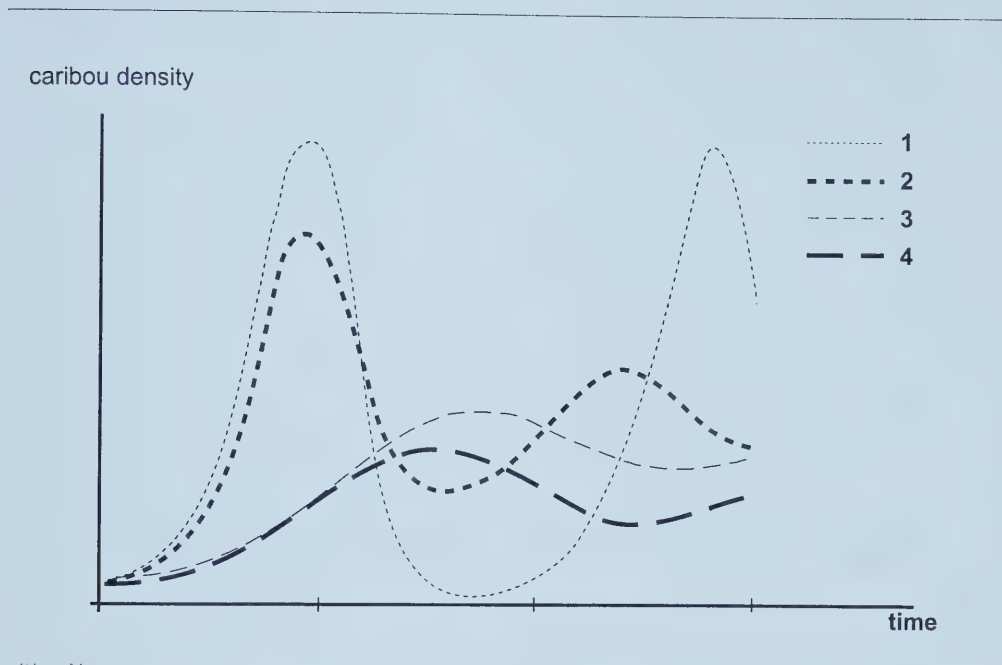
Figure 3.20. Patterns of caribou dynamics generated by REMUS for woodland caribou in Alberta, and proposed by Messier *et al.* (1988) for the George River Caribou Herd. **1** – projected dynamics for the George River Caribou Herd when r = 0.10 (Messier *et al.* 1988); **2** – woodland caribou dynamics in the system with no predation and lichen K = 870 kg /ha; **3** – projected dynamics for the George River Caribou Herd when r = 0.05 (Messier *et al.* 1988); **4** – woodland caribou dynamics in the system with no predation and lichen K = 730 kg /ha.
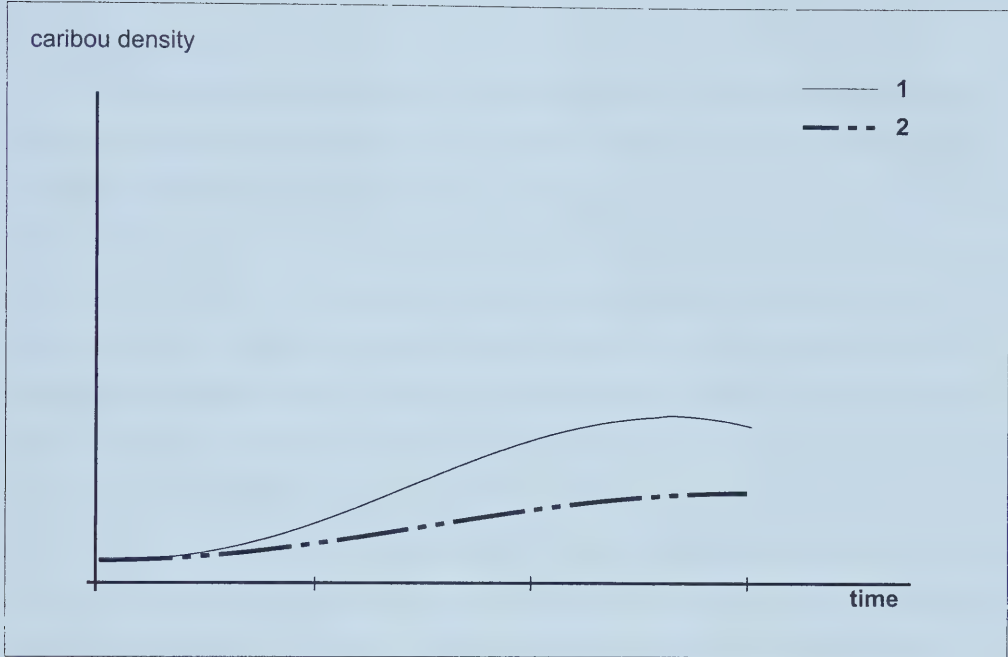
Figure 3.21. Projected dynamics for the George River Caribou Herd when r = 0.035 (Messier *et al.* 1988) – **1**; Woodland caribou dynamics generated in REMUS simulations in the system with wolf density = 0.008 wolf /km^2 and lichen K = 870 kg /ha – **2**.

Chapter IV
EFFECTS OF HUMAN ACTIVITY ON THE WOODLAND CARIBOU
SYSTEM

4.1. Introduction

Woodland caribou (*Rangifer tarandus caribou*) in Alberta exist at very low
densities (Edmonds 1988, Fuller and Keith 1981, Stuart-Smith *et al.* 1997). Recent
population monitoring suggests that most caribou populations in Alberta are declining
(Dzus 2001). Moreover, the caribou range in Alberta has shrunk significantly over
time (Edmonds 1991). The concerns about the low density of caribou led to a
threatened classification under the Alberta Wildlife Act in 1987 (Alberta Wildlife
Management Division 1996). At the same time industrial development continues on
caribou habitat. It is also known that human-built structures and linear corridors affect
the behavior of wildlife species (Horejsi 1979, Jalkotzy *et al.* 1997). Recently, it has
been shown that roads (Dyer 1999, Oberg 2001) and seismic lines (Dyer 1999) cause
caribou to avoid of good quality habitat in proximity of these structures. Dyer (1999)
stated that up to 48 % of habitat could be avoided by caribou in his study area in
northern Alberta due to the industrial impact on caribou range. This could decrease
habitat-based carrying capacity of the ecosystem. James (1999) and James and Stuart-
Smith (2000) reported that caribou that are closer to linear corridors are at higher risk
of being killed by wolves. Industrial and natural factors such as productivity of
habitat and natural predation from wolves (*Canis lupus*) and black bears (*Ursus
americanus*) act cumulatively in space and time.

Although there is no clear evidence that industrial development causes
caribou population declines (Bergerud *et al.* 1984), it is believed that direct habitat
loss or functional habitat loss due to habitat avoidance could lead to reductions of
caribou populations (Horejsi 1979, Jalkotzy *et al.* 1997). Many authors recommend
examining the demography of caribou (Dyer 1999, Horejsi 1979, Jalkotzy *et al.*
1997), in order to quantify the effect of industrial activity on caribou. A procedural
guide for oil and gas industry called Information Letter 91-17 states that petroleum
and gas exploration and development activities can occur on caribou range provided

that the integrity of the habitat is maintained to support its use by caribou (Alberta Department of Energy 1991). Dyer (1999) argued that functional habitat loss resulting from caribou avoidance of industrial infrastructures indicates that the goal set by IL 91-17 is not being met. Yet, it is not known whether this causes caribou declines.

The aim of my study was two-fold. First, in computer simulation experiments I attempted to predict the future dynamics of caribou population under conditions presently observed in the boreal ecosystem in northern Alberta. The second objective was to establish thresholds for alteration of caribou habitat by industrial activities such as creation of seismic lines, roads and oil wells under specific management scenarios (different levels of wolf control and moose (*Alces alces*) hunting), and different lichen carrying capacity in caribou habitat. I define a threshold for industrial impact on caribou as the density of industrial infrastructure (seismic lines, roads, and oil wells) at which caribou population remains stable around the presently observed density of 0.07 /km^2 (Stuart-Smith *et al.* 1997).

This research was conducted under the Boreal Caribou Research Program (BCRP), a research group, dedicated to generating scientific knowledge about caribou ecology and the boreal ecosystem. This information is used to integrate industrial land-use guidelines with caribou conservation.

4.2. Methods

For simulating the dynamics of caribou in response to varying forage resources, wolf predation and habitat alteration, I used the computer simulation model REMUS described in Chapter 2. As the size of the simulated area I used 20 000 km^2 and decided that 78% of this area is lowland habitat used by caribou. This estimation was based on the description of the study area reported by James (1999). I assumed that availability of plants dropped to zero in winter and that snow did not affect caribou access to lichens. The fire component of the model was turned on in all

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simulations. This resulted in 12 to 25% of lowland habitat being unsuitable for foraging by caribou (see Chapter 2 for explanation). Fire was a stochastic element of the model. In order to make the impact of cumulative effects of forage resources, predation and habitat alteration easier to interpret from the outputs of the simulations, the random variation of fire was drawn only once by the model and next this same sequence of fire occurrence was repeated in all simulation runs. All simulations were done for a period of 200 years. The initial density of caribou was set to 0.07 /km^2 (Stuart-Smith *et al.* 1997), moose to 0.25 /km^2 (Schneider and Wasel 2000) and wolves to 0.008 /km^2 (Gunson 1992). I assumed that linear corridors did not affect prey encounter rate and thus did not have direct effect on wolf predation. The above model settings were used in all simulation runs described in this chapter. Other controls of the model used in the simulations to test the effects of specific scenarios were set as follows:

4.2.1. Business as usual

I assumed that forage carrying capacity (K) in caribou habitat was 240 and 870 kg /ha for vascular plants and lichens respectively (Thomas and Kiliaan 1998). Based on data reported by BCRP (2000) I calculated annual human harvest of caribou to be around 0.8% of the total adult population, and used it in the model as input into the human harvest control (adult caribou annual survival is around 90.15% (from 85.1 to 95.2 %) and 8% of adult caribou mortalities are caused by hunting/poaching (BCRP 2000)). Bear predation on caribou in Alberta is poorly understood. To simulate caribou mortalities caused by bears I set the bear predation control to 0.03, which corresponded to 3% of the total adult caribou population being killed by bears annually (see Ballard 1994 for a review of black bear predation on caribou). Both human harvest and bear predation were subject to random fluctuations within the range of ±1.5% (Chapter 2). I assumed that wolves were uncontrolled and could increase in response to prey availability as determined by wolves' numerical response (Chapter 2) and that their social spacing behavior kept wolf population at a density not higher than 0.0587 /km^2 (Messier 1994). Wolf predation changed dynamically based on wolves' numerical and functional responses to total prey density (Chapter 2)

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and affected all caribou age classes. I also assumed that moose (the main prey for wolves) were hunted (bulls and cows equally) and moose hunting was around 20% of the total adult population (Alberta Environmental Protection 2001). As the input for habitat alteration I set the density of roads to 0.039 km /km^2, seismic lines to 1.185 km /km^2, and oil wells to 0.27 /km^2 as reported by Dyer (1999) in his study area. I used 4 and 8 meters as average widths of seismic lines and roads respectively. These were underestimated widths as the conventional seismic lines are usually 8 meters wide (Jalkotzy *et al.* 1997, Osko 2001). I underestimated the widths of seismic lines to account for the potential implementation of low-impact seismic lines in caribou habitat in the future. Based on the findings by Dyer (1999) I decided that caribou used habitat in proximity to the above structures less than expected. I used four different buffers (100 m, 250 m, 500 m, and 1000 m) around roads and seismic lines, and three buffers around oil wells (100 m, 250 m, 1000m). Habitat avoidance in each buffer was set according to Dyer (1999). Consequently, habitat avoidance differed with season and was strongest in winter when up to 40% of the total area was avoided, habitat reduced use in buffers around roads was stronger than around seismic lines (Dyer 1999). I assumed that habitat alteration was static, i.e. the densities of roads, seismic lines and oil wells did not change over time (the regeneration rate of old structures was the same as the rate of creation of new ones).

4.2.2. Thresholds for industrial activity under different wildlife management options

To establish thresholds specific for different management options (wolf control, reductions of moose) and varying ecosystem productivity (lichen K), I looked at caribou population dynamics in the system with the following management options:

(1) no predation – the initial density of wolves was set to zero, which resulted in total exclusion of wolves from the system for the entire simulation (Chapter 2);

(2) uncontrolled wolf predation and uncontrolled moose population – neither
    moose nor wolves were hunted;

(3) uncontrolled wolf predation and moose population reduced by human harvest
    of 40% of adults annually;

(4) uncontrolled wolf predation and moose population reduced by human harvest
    of 60% of adults annually;

(5) wolf population controlled at the maximum density of 0.004 /km^2 and
    uncontrolled moose population;

(6) wolf population kept at the maximum density of 0.004 /km^2 and moose
    population reduced by human harvest of 40% of adults annually;

(7) wolf population kept at the maximum density of 0.004 /km^2 and moose
    population reduced by human harvest of 60% of adults annually;.

Runs for all the above seven model settings were done for three different
values of lichen carrying capacity (K): 730, 870 and 1305 kg /ha, and for two settings
of caribou behavior in relation to human-built structures: 1) caribou did not avoid
habitat close to human-built structures; 2) caribou used habitat near linear corridors
and oil wells less than expected, and the level of avoidance was adjusted according to
Dyer (1999), as described in section 4.2.1. First, I set the densities of roads to 0
km/km^2 and oil wells to 1 /km^2, and looked for the density of seismic lines at which
caribou were stable at 0.07/km^2. Next, I gradually increased the density of roads to
0.1 and 0.2 km/km^2 and looked for the threshold density of seismic lines. Finally, I
looked for the threshold density of seismic lines when the density of oil wells was set
to 0.05 /km^2 and roads to 0 /km^2.

In all seven scenarios I assumed that there was no human harvest of caribou
(hunting/poaching) and that black bears were not significant predators (bear predation
control set to 0). In (2), (3) and (4) wolves could potentially increase to the maximum
density of 0.0587 /km^2, if this should be exceeded wolves dispersed from the system,
so that the wolf density would never be higher than 0.0587 /km^2 (uncontrolled wolf
population).

4.3. Results

4.3.2. Business as usual

Caribou declined very sharply during the first 15 years and dropped to an extremely low density of 0.02 /km^2 (which is a total number of 400 caribou in an area of 20 000 km^2) in the 16th year. Next, the decline was less dramatic, but caribou still declined. Caribou were extirpated from the system in the 37th year of the simulation (Figure 4.1).

4.3.3. Thresholds for industrial activity under different wildlife management options

The outputs of the simulations are summarized in Tables 4.1 to 4.8. The limited data on lichen carrying capacity (K) in caribou habitat in northern Alberta (Chapter 2) suggests that K may be close to 870 kg /ha. Consequently, the thresholds reported for this level of lichen K are the most likely (Table 4.8). In all seven simulated management options habitat avoidance had very strong impact on the thresholds. The outputs of the simulations for the seven management options were as follows:

(1) If wolves were excluded from the system and with no habitat avoidance caribou could deal with 40 km /km^2 of linear corridors (20 km /km^2 of seismic lines and 20 km /km^2 of roads). This threshold dropped to just 1.65 km /km^2 (24-fold) if caribou used habitat close to linear corridors less than expected (Table 4.1).

(2) Introduction of an uncontrolled wolf population had strong effect on thresholds: assuming no habitat avoidance caribou were stable with 14 km /km^2 of linear corridors (7 km /km^2 of seismic lines and 7 km /km^2 of roads; 2.86-fold decrease from the system with no predation), but only 0.3 km/km^2 of seismic lines and no roads could be cut if habitat reduced use was simulated. This was 47-fold decrease (from 14 to 0.3 km/km^2) in the threshold due to habitat avoidance (Table

4.2) and 5.5-fold decrease due to predation (1.65 km/km^2 of seismic lines without predation and 0.3 km/km^2 if uncontrolled wolves present).

(3) Reducing adult moose population by 40% annually with uncontrolled wolf predation allowed more linear corridors: caribou were stable at the total density of roads and seismic lines = 26 km/km^2 (13 km /km^2 of seismic lines and 13 km /km^2 of roads) with no habitat avoidance, and at 1 km/km^2 of seismic lines when habitat avoidance was simulated (Table 4.3).

(4) More significant reduction of adult moose (harvesting 60% annually) produced the highest thresholds for linear corridors. The total density of roads and seismic lines equal to 30 km/km^2 (15 km /km^2 of seismic lines and 15 km /km^2 of roads) with no habitat avoidance, or 1.2 km/km^2 of seismic lines with habitat avoidance, no roads and 0.05 oil wells /km^2 resulted in a stable caribou population (Table 4.4).

(5) Wolf control (wolves kept at 0.004 /km^2) alone was less efficient in increasing the thresholds for linear corridors (density of linear corridors = 20 km/km^2 with no avoidance, and seismic lines at 0.8 km/km^2 with habitat avoidance) than significant moose reductions (Table 4.5).

(6) Wolf control (wolves kept at 0.004 /km^2) accompanied by harvesting 40% of the adult moose population did not change the thresholds produced when moose reduction was applied alone (3) (Tables 4.6 and 4.8).

(7) Simulation of simultaneous wolf control (wolves maximally at 0.004 /km^2) and significant reduction of moose (harvesting 60% of adults annually) produced the same thresholds as reductions of moose applied alone (4) (Tables 4.7 and 4.8).

4.4. Discussion

4.4.1. General comments

The present work is the first attempt to assess the cumulative effects of both natural and human-induced factors on woodland caribou population dynamics in northern Alberta in simulation experiments. If the present conditions in the boreal

ecosystem do not change, the model predicts dramatic decline in caribou population over the next several years in ranges with the density of linear corridors equal to or higher than 1.224 km/km^2. The model suggests that in order to save woodland caribou from extirpation in northern Alberta, decisive modifications of the current land use need to be made as soon as possible. According to REMUS simulations continuing business as usual would lead to the reduction of caribou numbers by 50% in 15 years, and the species would be extirpated in less than 40 years (Figure 4.1) in areas with 1.224 km of linear corridors per 1 km^2. This is also true if wolf density does not exceed 0.008 /km^2 as reported by Gunson (1992) (Figure 4.2). I believe the above outputs are the most optimistic because of the following reasons: 1) caribou calves were neither hunted/poached or killed by bears and other natural predators different than wolves; 2) the density of human-built structures did not increase over time; 3) widths of linear corridors were underestimated; 4) simulated maximum functional habitat loss due to avoidance was slightly less (40%) than reported by Dyer (1999) (48%). 5) I assumed that linear corridors did not affect prey encounter rate and thus did not have direct effect on wolf predation. The above five assumptions resulted in showing less caribou mortality and less loss of habitat.

Based on the outputs of the simulations I refute Bergerud's (1988, 1996) statement that caribou can deal with industrial development on their range if wolf densities are lower than 0.0065 /km^2. I argue that whether caribou are able to persist in the system depends on the cumulative effects of predation, wolf-prey interactions, productivity of the ecosystem and the impact of industry (Tables 4.1 to 4.7) and relative changes in the aforementioned factors. REMUS simulations predict that woodland caribou in Alberta can coexist at presently observed low density (0.07 /km^2) with uncontrolled wolf population (density > 0.0065 /km^2) if the density of linear corridors does not exceed 0.3 km /km^2 of seismic lines and 0 km /km^2 of roads. If wolves are reduced by more than 50% (from 0.0087 to 0.004 /km^2) and assuming that there is no human harvest of caribou and bear predation is insignificant, the threshold for linear corridors is 0.8 km /km^2 of seismic lines and nil for roads. Based on the model's simulations, the present impact of industry on caribou habitat in

northern Alberta is already too strong to allow caribou to persist in the system with wolf population controlled at 0.004 /km². If wolves are totally excluded from the ecosystem, and assuming that caribou avoid human-built structures as described by Dyer (1999) the maximum threshold for linear corridors on caribou range is 1.65 km/km² of seismic lines with no roads, or less then that with roads (Table 4.1). Dyer (1999) reported the density of linear corridors in his study area to be 1.224 km /km². This shows that we are close to reaching the thresholds for linear corridors even if wolves are completely removed from the system. This in turn implies that wolf control is not a solution for caribou recovery or even maintaining the population at the present density.

I believe that, as in the 'business as usual' section, the seven simulated management options predicted more optimistic outcomes than should be expected in the real ecosystem. The reasons are as follows: 1) the assumption was made that bears were insignificant predators; 2) human harvest was assumed to be negligible; 3) widths of linear corridors were underestimated; 4) the model design described the maximum avoidance to be 40% of the total habitat, which is less than reported by Dyer (1999) (up to 48%); 5) I assumed that linear corridors did not affect prey encounter rate and thus did not have direct effect on wolf predation. The above five assumptions resulted in showing less caribou mortality and less loss of habitat.

One could suspect that both actual and functional habitat loss should reduce the habitat-based carrying capacity of the ecosystem (HK) and thus lead to population declines. Consequently, examining the effects of the habitat loss caused by direct habitat alteration and caribou behavioral responses was recommended by several authors (Horejsi 1979, Dyer 1999, Jalkotzy 1997). Dyer (1999) noted that no attempt was made to assess the consequences of habitat loss on caribou demographics.

I modeled the behavioral response of caribou to development corridors by simulating avoidance. Direct mortality (vehicle collisions) and indirect mortality (increased human harvest and increased wolf predation) were not simulated. Yet,

population-level effects were evident in the outputs of the simulations. Then, one could argue that if factors such as direct and indirect mortalities were included, the detrimental effect on the population would be even stronger.

The outputs of the simulations summarized in Tables 4.1 – 4.8 show clear difference in thresholds between road density and seismic line density. This was caused by simulating roads as having a stronger impact on caribou behavior than seismic lines. This component of the model was based on the findings by Dyer (1999) and was consistent with the assessments by Horejsi (1979) and Jalkotzy *et al.* (1997).

The outputs of the simulations suggest that in order to keep wolf population at densities lower than 0.004 /km^2 (without direct wolf control) around 60% of adult moose should be harvested annually. It is believed that moose populations would decline if 20% of cows are harvested annually (Alberta Environmental Protection 2001). Consequently, harvesting 60% annually should cause a dramatic crash in moose population. Indeed, abrupt and deep decreases in moose populations would be needed in order to produce very sharp decline in wolves. If wolves do not decline rapidly enough, reduced availability of the main prey (moose) could increase wolf predation on caribou. To describe this process fully, spatial modeling accounting for the relative distribution of the three species is needed.

Still, one could suspect that annual removal of 60% of adult moose could result in continuous decline of moose population. One could calculate, assuming equal sex ratio in the moose population, that it can increase by the maximum of 100% annually if all cows twin. Certainly, not all cows twin every year, but at the same time sex ratio in a hunted ungulate populations is usually unequal with more females being present in the population. This increases the potential percent by which the population can grow. Moreover, in the simulations an assumption was made that the main predator preying on moose is wolf, and black bears have an unmeasurable effect on moose dynamics. Although the effects of bear predation on moose populations are poorly understood (Boutin 1992), one could expect that bears by preying on moose

calves could potentially have measurable negative impact on moose population growth. In a real situation one needs to consider bear predation on moose. Then, in order to significantly reduce wolves (below the density of 0.004 /km^2), a moose harvest of less than 60% of all adults should be sufficient.

Table 4.8 provides an interesting comparison of the effects of different management options on the thresholds for industrial developments. Assuming the same carrying capacity of forage, these thresholds depend mostly on wolf predation pressure that differs according to specific management scenarios (Figure 4.3). If wolves are not controlled and 40 % of adult moose population is harvested annually, wolf density is close to 0.004 /km^2 and periodically drops below that. Consequently, both harvesting 40% of adult moose alone, and this level of moose harvest with assumed wolf control at the density of 0.004 /km^2 produce similar thresholds for industrial infrastructure. Wolf control (at 0.004 /km^2) applied without reductions of moose (management option No. 5), results in keeping wolves at the constant density of 0.004 /km^2. And this in turn produces lower thresholds for industrial development than moose reductions. Similar reasoning applies to management options 4 and 7. Drastic reductions of moose (60 %) cause wolf population to be below the density of 0.004 /km^2 most of the time. Consequently, options 4 and 7 produce very similar thresholds.

4.4.2. The influence of linear corridors on wolf predation

One of the goals of this modeling research was to address the question how linear corridors affect wolf predation on caribou. In Chapter 2 I proposed a mechanism for a model that could target the issue. To use this model, a number of elements need to be described with factual data. The mechanism consists of 10 elements: A - relative use of linear corridors by caribou; CM - changes in caribou mobility due to snow conditions; H - human use of linear corridors; L - the density of linear corridors (km/km^2); S - snow depth; TS - wolves' travel speed on linear corridors; TRD - threshold road density above which wolves do not use specific area; U - relative use of linear corridors by wolves; and W - wolf density. The interactions of the above variables would impact prey encounter rate on linear corridors (ER$_{LC}$),

which in turn influences predation efficiency (D). The variables that could be estimated on the base of existing data obtained from field experiments are: threshold road density for wolves (TRD) (Thurber *et al.* 1994, Thiel 1985), density of linear corridors (L) – the data from Dyer's work (1999) could be used, or any desired density could be entered to test its effect; changes in caribou mobility (CM) (Schneider *et al.* 2000); wolves' travel speed on linear corridors (TS) could be estimated from the findings of James (1999) and Musiani *et al.* (1998). The variable A (relative use of linear corridors by caribou) could be estimated from Dyer's (1999) findings. However, I believe that caribou avoidance of linear corridors may be determined by wolf density (W), wolf use of linear corridors (U), and human use (H) of linear corridors (Chapter 2). Moreover, it is known that the effect of predation (e.g. wolf density) on selection of movement paths by caribou (variable A) is scale dependent (Johnson 2000). Furthermore, Dyer (1999) listed six factors that influence caribou response to human activities (type of disturbance, frequency of disturbance, an animal's physical condition, reproductive condition, sex, and effects of vegetation and topography) that would in turn affect variable A. This complicates estimating variable A even more (for a literature review of the effects of linear corridors on caribou behavior see Dyer 1999, Jalkotzy *et al.* 1997 and Oberg 2001). Wolf density (W) is an internal variable of the model and does not need to be estimated by the user of the model. However, variables U and H are not supported by any reliable data from field experiments and as such are highly speculative. Consequently, three key variables (A, H, U) cannot be estimated.

The part of REMUS describing the effects of linear corridors on wolf predation could potentially have significant impact on the outputs of the simulations. For example, if avoidance of linear corridors is very weak or absent, the threshold for linear corridors would be 14 km/km^2 (management option No. 2). This is more than the threshold road density reported for wolves (Thiel 1985, Thurber *et al.* 1994). According to Thiel (1985) and Thurber *et al.* (1994), predation would be absent when road density exceeds 0.6 km/km^2. Consequently, in the range of linear corridors from 0.6 to 14 km /km^2 increase in caribou numbers could be observed.

If caribou avoid industrial infrastructure, and if this avoidance is strong enough (avoidance of up to 1000 meters recorded by Dyer (1999)), linear corridors would not increase wolves' prey encounter rate and thus would not have any effect on wolf-caribou interaction. Instead, habitat avoidance (up to 48% of the total habitat in Dyer's (1999) study area) could have significant negative impact on habitat-based carrying capacity of the boreal ecosystem. Moreover, habitat avoidance would compress existing caribou on a much smaller area. Woodland caribou evolved behaviorally to space out to decrease the probability of being found by a predator (Bergerud *et al.* 1984). Thus, compressing them on a smaller area could cause dispersion and consequently increase encounter rate with predators. This, combined with decreased habitat-based carrying capacity, would result in decrease in caribou numbers. The above reasoning indicates that the mechanism for the effects of linear corridors on predation is much more complex than the simple design proposed in Chapter 2. Many elements of this complex process need to be described by data from field experiments.

I believe that as long as all elements of the mechanism for the effects of linear corridors on wolf predation proposed in Chapter 2 are not supported by factual data, produced outputs cannot be used as reliable information. Therefore, I decided not to include this section of REMUS in simulations described in this thesis and to discuss their meaning.

4.4.2. Management implications

Based on the simulations completed in REMUS, the following statements can be made:
1) The thresholds for industrial development on some caribou ranges in northern Alberta may already be exceeded – model predicts that in areas with 1.224 km of linear corridors per km^2 caribou numbers would be reduced by 50% in 15 years, and the species would be extirpated in less than 40 years.

2) If there is no predation and no avoidance of linear corridors, caribou are able to deal with very high impact of industry (the threshold is 40 km of linear corridors per 1 km^2).

3) The threshold from (2) drops significantly if caribou show avoidance of linear corridors. All management practices that reduce caribou avoidance of industrial infrastructure are of highest importance in caribou conservation.

4) Significant reductions in moose may be more beneficial for caribou than direct wolf control. I need to stress here, that in order to recommend this management action, a spatial model describing the spatial distribution of wolves, moose and caribou and accounting for the Spatial Separation Hypothesis (James 1999) needs to be developed to simulate the effects of relative distribution of the three species on wolf-caribou interaction.

5) Wolf control is not a viable solution because:

    a) If wolves are reduced to just 0.004 /km^2 (by more than 50% assuming the present density to be 0.0087 /km^2 (Gunson 1992)) and assuming that there is no human harvest of caribou and bear predation is insignificant, the threshold for linear corridors is 0.8 km /km^2. Dyer (1999) reported the density of linear corridors in his study area to be 1.224 km/km^2. Consequently, even reduction of wolves by more than 50% would not stop caribou decline;

    b) If wolves are totally excluded from the ecosystem, and assuming that caribou avoid human-built structures as described by Dyer (1999) the maximum threshold for linear corridors on caribou range is 1.65 km/km^2 of seismic lines with no roads and less than that with roads. In some caribou ranges the density of linear corridors is close to this threshold.

6) I think it is very important to increase people's awareness of caribou conservation. By educating and informing people about caribou status, we could reduce human-caused caribou mortality due to hunting/poaching. If people were not perceived as predators caribou would likely habituate to human presence. In such a case increased human activity on linear corridors might be beneficial to caribou by reducing natural predation. It is known that ungulates if not threatened directly by people can be attracted by human developments that provide refuge from predators (Banff-Bow Valley Study 1996).

7) Immediate changes in land use practices and wildlife management actions need to be undertaken as soon as possible. The most beneficial to caribou seem to be:

    a) low-impact seismic lines (only if research shows that they are neither avoided by caribou nor increase predation rate);

    b) significant reductions in moose population (annual harvest of 60% of the total adult population) in areas where caribou populations are being managed.

4.4.3. Research needed

Simulations completed in REMUS indicate that the most crucial research needed in caribou conservation is in the following areas:

1) There is not enough data to draw conclusions based on REMUS simulations on the effects of linear corridors on predation by wolves on caribou. There is a need to fill the blank elements in the model design describing the effect of linear corridors on predation presented in Chapter 2. As the caribou avoidance of good quality habitat seems to be the most detrimental to caribou population dynamics, it needs to be examined in close detail to describe the mechanism that governs it. Such elements as human activities on linear corridors and caribou habituation to people and industrial infrastructure seem to be the drivers for the influence of linear corridors on wolf-

caribou interactions. It is known that in Poland, where the density of linear corridors (forest division lines) is around 1 km /km^2 wolves hunt further from linear corridors (Jedrzejewska pers. comm.). Consequently, linear corridors could be selected by ungulates as refuge from predation. Indeed, ungulate density in Eastern Europe is very high (Jedrzejewska *et al.* 1994), despite uncontrolled wolf population and substantial hunting pressure. The avoidance of linear corridors by wolves seems to be caused by presence of people on linear corridors. If this is also true for northern Alberta, human access could be one of the factors that shape wolf-caribou interactions on linear corridors. One could hypothesize that it might be beneficial for caribou to have more people on linear corridors as this could significantly reduce natural predation.

2) REMUS simulations produced different thresholds for industrial development on caribou range for specific levels of the ecosystem carrying capacity (biomass of lichens). As the data on the forage availability and productivity in the boreal ecosystem in Alberta is very limited, this is one of the key research gaps that needs to be addressed if one is to balance industrial development and caribou conservation in Alberta.

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Table 4.1. Threshold densities for industrial infrastructure (in km /km^2 for seismic lines and roads, and oil wells /km^2) under different productivity of the ecosystem (lichen K) and with two types of behavioral response of caribou to industrial developments (no avoidance and avoidance), assuming that there is **no natural predation** in the system, and **moose are not harvested**. **Caribou are not hunted/poached** (management option No. 1).

| Lichen K | No Avoidance | | | Avoidance | | |
	Roads	Seismic Lines	Oil Wells	Roads	Seismic Lines	Oil Wells
1305	37	37	37	0	2.65	1
				0.1	2.18	1
				0.2	1.65	1
				0	2.75	0.05
870	20	20	20	0	1.5	1
				0.1	1.1	1
				0.2	0.6	1
				0	1.65	0.05
730	9	9	9	0	0.9	1
				0.1	0.4	1
				0.2	0	1
				0	0.95	0.05

Table 4.2. Threshold densities for industrial infrastructure (in km /km^2 for seismic lines and roads, and oil wells /km^2) under different productivity of the ecosystem (lichen K) and with two types of behavioral response of caribou to industrial developments (no avoidance and avoidance), assuming that there is **uncontrolled wolf population** in the system (the maximum potential wolf density = 0.059 /km^2), and **moose are not harvested**. **Caribou are not hunted/poached** (management option No. 2). "Exceeded" means that under given conditions caribou decline if the density of seismic lines is 0 km /km^2 or more.

	No avoidance			Avoidance		
Lichen K	Roads	Seismic Lines	Oil Wells	Roads	Seismic Lines	Oil Wells
1305	22	22	22	0	1.6	1
				0.1	1.2	1
				0.2	0.6	1
				0	1.8	0.05
870	7	7	7	0	0.1	1
				0.1	exceeded	1
				0.2	exceeded	1
				0	0.3	0.05
730	0	exceeded	0	0	exceeded	0

Table 4.3. Threshold densities for industrial infrastructure (in km /km^2 for seismic lines and roads, and oil wells /km^2) under different productivity of the ecosystem (lichen K) and with two types of behavioral response of caribou to industrial developments (no avoidance and avoidance), assuming that there is **uncontrolled wolf population** in the system (the maximum potential wolf density = 0.059 /km^2), and **40% of the adult moose are harvested** every year. **Caribou are not hunted/poached** (management option No. 3). "Exceeded" means that under given conditions caribou decline if the density of seismic lines is 0 km /km^2 or more.

Lichen K (kg / ha)	No avoidance			Avoidance		
	Roads	Seismic Lines	Oil Wells	Roads	Seismic Lines	Oil Wells
1305	31	31	31	0	2.2	1
				0.1	1.7	1
				0.2	1.2	1
				0	2.3	0.05
870	13	13	13	0	0.8	1
				0.1	0.3	1
				0.2	exceeded	1
				0	1	0.05
730	3	3	3	0	exceeded	1
				0.1	exceeded	1
				0.2	exceeded	1
				0	0.2	0.05
				0.05	0	0.05

Table 4.4. Threshold densities for industrial infrastructure (in km /km^2 for seismic lines and roads, and oil wells /km^2) under different productivity of the ecosystem (lichen K) and with two types of behavioral response of caribou to industrial developments (no avoidance and avoidance), assuming that there is **uncontrolled wolf population** in the system (the maximum potential wolf density = 0.059 /km^2), and **60% of the adult moose are harvested** every year. **Caribou are not hunted/poached** (management option No. 4). "Exceeded" means that under given conditions caribou decline if the density of seismic lines is 0 km /km^2 or more.

| Lichen K | No avoidance | | | Avoidance | | |
	Roads	Seismic Lines	Oil Wells	Roads	Seismic Lines	Oil Wells
1305	33	33	33	0	2.35	1
				0.1	1.85	1
				0.2	1.35	1
				0	2.5	0.05
870	15	15	15	0	1	1
				0.1	0.55	1
				0.2	0.15	1
				0	1.2	0.05
730	7	7	7	0	exceeded	1
				0.1	exceeded	1
				0.2	exceeded	1
				0	0.45	0.05

Table 4.5. Threshold densities for industrial infrastructure (in km /km^2 for seismic lines and roads, and oil wells /km^2) under different productivity of the ecosystem (lichen K) and with two types of behavioral response of caribou to industrial developments (no avoidance and avoidance), assuming that **wolf control is in effect** (the maximum potential wolf density = 0.004 /km^2), and **moose are unhunted**. **Caribou are not hunted/poached** (management option No. 5). "Exceeded" means that under given conditions caribou decline if the density of seismic lines is 0 km /km^2 or more.

Lichen K	No Avoidance			Avoidance		
	Roads	Seismic Lines	Oil Wells	Roads	Seismic Lines	Oil Wells
1305	29	29	29	0	2.1	1
				0.1	1.6	1
				0.2	1.1	1
				0	2.25	0.05
870	10	10	10	0	exceeded	1
				0.1	exceeded	1
				0.2	exceeded	1
				0	0.80	0.05
730	1	1	1	0.01	0	0.05

Table 4.6. Threshold densities for industrial infrastructure (in km /km^2 for seismic lines and roads, and oil wells /km^2) under different productivity of the ecosystem (lichen K) and with two types of behavioral response of caribou to industrial developments (no avoidance and avoidance), assuming that **wolf control is in effect** (the maximum potential wolf density = 0.004 /km^2), and **40% of adult moose are harvested** annually. **Caribou are not hunted/poached** (management option No. 6). "Exceeded" means that under given conditions caribou decline if the density of seismic lines is 0 km /km^2 or more.

Lichen K	No avoidance			Avoidance		
	Roads	Seismic Lines	Oil Wells	Roads	Seismic Lines	Oil Wells
1305	29	29	29	0	2.1	1
				0.1	1.65	1
				0.2	1.2	1
				0	2.25	0.05
870	10	10	10	0	0.7	1
				0.1	0.2	1
				0.2	exceeded	1
				0	0.8	0.05
730	1	1	1	0	exceeded	1
				0.1	exceeded	1
				0.2	exceeded	1
				0	0.1	0.05

Table 4.7. Threshold densities for industrial infrastructure (in km /km^2 for seismic lines and roads, and oil wells /km^2) under different productivity of the ecosystem (lichen K) and with two types of behavioral response of caribou to industrial developments (no avoidance and avoidance), assuming that **wolf control is in effect** (the maximum potential wolf density = 0.004 /km^2), and **60% of adult moose are harvested annually**. **Caribou are not hunted/poached** (management option No. 7). "Exceeded" means that under given conditions caribou decline if the density of seismic lines is 0 km /km^2 or more.

	No avoidance			Avoidance		
Lichen K	Roads	Seismic Lines	Oil Wells	Roads	Seismic Lines	Oil Wells
1305	33	33	33	0	2.3	1
				0.1	1.9	1
				0.2	1.4	1
				0	2.5	0.05
870	15	15	15	0	1.1	1
				0.1	0.6	1
				0.2	0.1	1
				0	1.2	0.05
730	6	6	6	0	exceeded	1
				0.1	exceeded	1
				0.2	exceeded	1
				0	0.5	0.05

Table 4.8. Thresholds (caribou stable around 0.07 /km^2) for the density of industrial infrastructure with lichen carrying capacity (K) = 870 kg/ha, and habitat avoidance as reported by Dyer (1999), resulting from seven management options. All assume that caribou are not hunted/poached. "Exceeded" means that under given conditions caribou decline if the density of seismic lines is 0 km /km^2 or more.

Management option	Roads (km / km^2)	Seismic Lines (km / km^2)	Oil Wells (/ km^2)
1. No predation	0	1.5	1
	0.1	1.1	1
	0.2	0.6	1
	0	1.65	0.05
2. Uncontrolled wolf predation	0	0.1	1
	0.1	exceeded	1
	0.2	exceeded	1
	0	0.3	0.05
3. Uncontrolled wolf predation and moose reduced by 40% annually	0	0.8	1
	0.1	0.3	1
	0.2	exceeded	1
	0	1	0.05
4. Uncontrolled wolf predation and moose reduced by 60% annually	0	.1	1
	0.1	0.55	1
	0.2	0.15	1
	0	1.2	0.05
5. Wolves controlled at 0.004 /km^2, no moose harvest	0	exceeded	1
	0.1	exceeded	1
	0.2	exceeded	1
	0	0.8	0.05
6. Wolves controlled at 0.004 /km^2 and moose reduced by 40% annually	0	0.7	1
	0.1	0.2	1
	0.2	exceeded	1
	0	0.8	0.05
7. Wolves controlled at 0.004 /km^2, moose reduced by 60% annually	0	1.1	1
	0.1	0.6	1
	0.2	0.1	1
	0	1.2	0.05
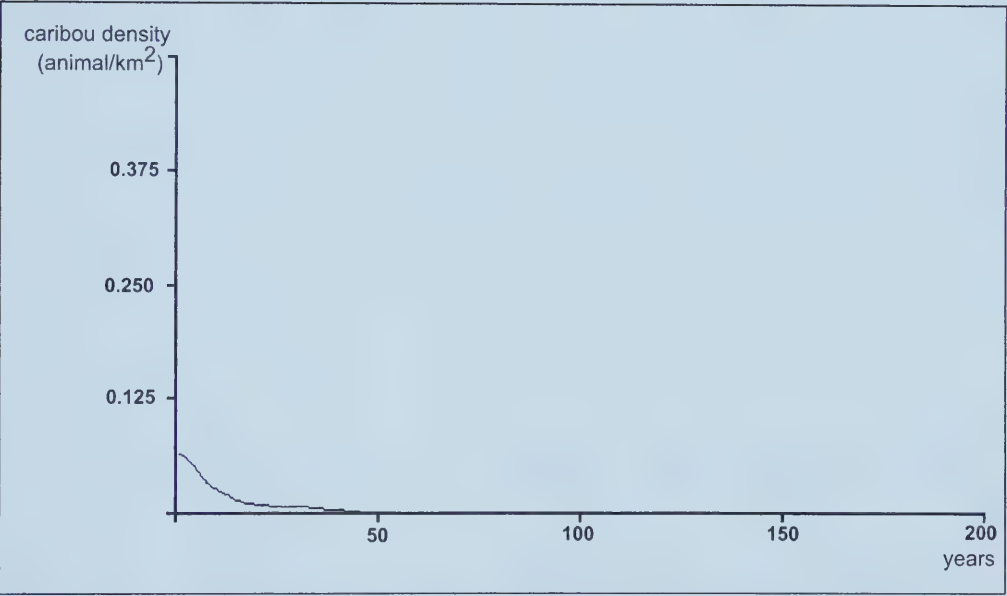
Figure 4.1. Caribou population dynamics under 'business as usual' conditions. Caribou initial density is 0.07 /km^2. Uncontrolled wolf population could reach the maximum potential density of 0.0587 /km^2 (Messier 1994). Density of linear corridors = 1.224 km /km^2.

Figure 4.2. Caribou population dynamics under 'business as usual' conditions. Caribou initial density is 0.07 /km². Uncontrolled wolf population stayed at the density of 0.0087 /km² (Gunson 1992). Density of linear corridors = 1.224 km /km².
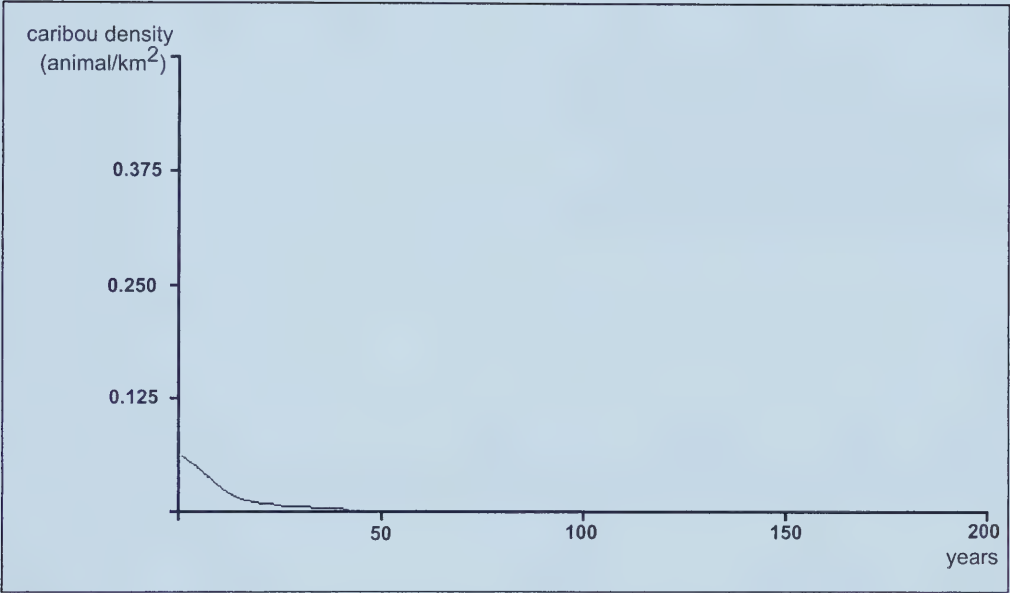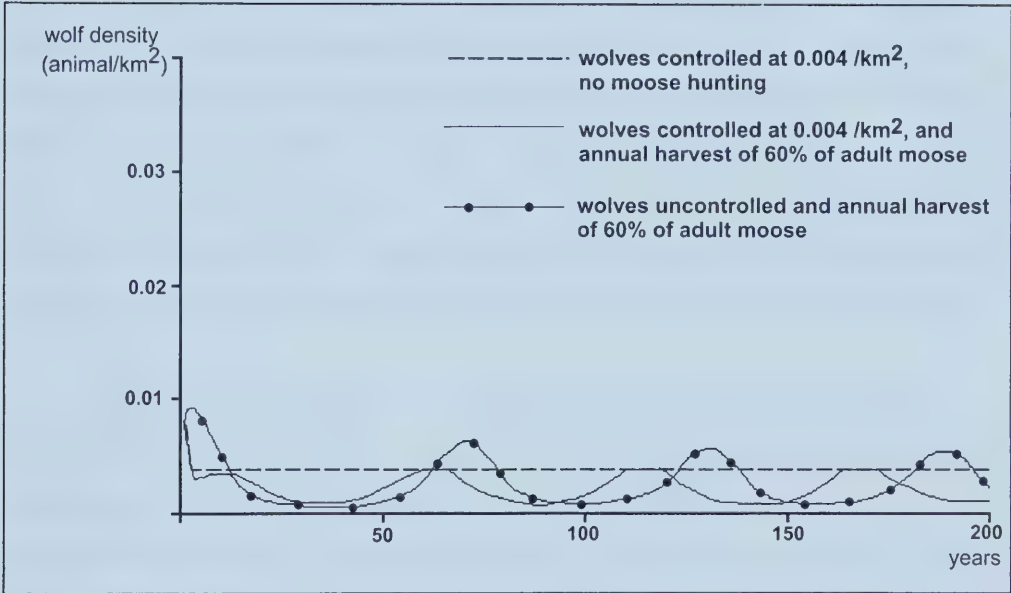
Figure 4.3. Dynamics of wolf population resulting from different management options. In all cases the initial density of wolves = 0.008 /km².

CHAPTER V
SYNTHESIS

The goal of the Boreal Caribou Research Program (BCRP) is to generate scientific knowledge about woodland caribou (*Rangifer tarandus caribou*) ecology, the boreal ecosystem and the effects of industrial activity on caribou. This information is used to develop industrial land-use guidelines with respect to caribou conservation. At the start of the BCRP, little was known about caribou in northern Alberta. Over a decade of intensive research extensive knowledge on caribou was gained. This allowed me to build a computer simulation model (REMUS) describing caribou population dynamics. Although the BCRP research was the main source of information for REMUS, literature relevant to caribou and the boreal ecosystem was consulted to fill gaps. Expert opinion of researchers having extensive experience on boreal ecology was also important in the decisions made when building the model.

Because models are holistic descriptions of the interactions among all elements of the dynamic entity, they allow their users to refine their understanding. Models can also be powerful educational tools for wildlife managers and stakeholders. Such a knowledge transfer role has recently been demonstrated by Dr. Brad Stelfox and his ALCES™ model (Forem Technologies 2001). ALCES™ is a model that simulates the dynamics of natural and anthropogenic disturbances on landscapes such as northern Alberta. REMUS was designed to translate landscape changes generated by ALCES into impacts on caribou populations.

The first task in the development of REMUS was to identify the key elements that shape caribou population dynamics. During the design phase, the model structure became more focused on the elements that seem to be the key variables that shape the dynamics of caribou. The next step was to decide how those elements interact, and to examine how the caribou system would behave in the natural ecosystem devoid of human intervention (Chapter 3). This could serve as a control when assessing the effects of industry. After that, I assessed cumulative effects on caribou dynamics (business as usual in Chapter 4). Finally, based on the outputs of the simulations, I

identified the factors having the strongest effect on caribou (Chapter 4) and proposed thresholds for industrial activity on caribou range. Patterns of population dynamics generated by REMUS were similar to those reported from field research, and to published mathematical models.

Models reflect the way in which people perceive the complex interactions that built the reality (Boyce 2000). Therefore, every model should be considered a complex hypothesis. REMUS is a hypothesis of how the boreal caribou system behaves. The outputs of the simulations and management recommendations based on them are hypothetical. Yet, they inform the decision-making process and guide research, the usual goals of natural resource models (Starfield 1997).

Simulations described in this thesis do not include all possible interactions and changes in the elements of the system that could be explored. REMUS includes controls that could be used to test the effects of differential harvest of cows and bulls (both caribou and moose (*Alces alces*), rate of change of certain industrial developments (linear corridors and oil wells), and varying effects of snow conditions on limiting caribou access to food. One could also manipulate the initial densities of all species to examine the effects of specific initial conditions on future dynamics.

5.1. Knowledge refinement and research needed

The process of model building and sensitivity analysis allowed me to identify critical uncertainties. I believe the most needed research is in the following areas (in order of decreasing importance):

1) *Available forage biomass*. Measurements of the total biomass of arboreal and terrestrial lichens, and vascular plants utilized by caribou are important, yet largely unavailable for the boreal plains of northern Alberta. Next, one should look at what percent of the total forage biomass is available to caribou, and finally, what percent of this available biomass can be potentially consumed by caribou (has nutritional value, is not decayed). To recommend mitigation in caribou habitat one needs to know the potential habitat-based caribou carrying capacity (HK)). REMUS

simulations produced different thresholds for industrial development on caribou range for each level of lichen carrying capacity. These simulations also indicated that HK affects the ability of caribou to deal with predation. Revegetation and regeneration of seismic lines are other factors that would certainly affect HK. Consequently, this is also a key research need.

2) *Functional loss of habitat.* REMUS simulations suggest that the most detrimental factor to caribou demography is the functional loss of habitat due to caribou avoidance of good quality (food) habitat in proximity of industrial infrastructures. I recommend research on the mechanism governing avoidance by caribou. Based on literature (Dyer 1999, Jalkotzy *et al.* 1997, Oberg 2001), it seems that the key elements are: type and frequency of disturbance, effects of vegetation and topography, changes in caribou mobility due to snow conditions, human use of linear corridors, caribou habituation to human presence, and relative use of linear corridors by wolves.

3) *Low-impact seismic lines.* Future research on the effects of low-impact seismic lines on caribou and wolf behavior and ecology (e.g. predator-prey interactions, habitat use) would allow expanding the model by adjusting its structure to account for new industry practices.

4) *Post-fire habitats.* Examining the importance of fire and burned sites in caribou ecology would be an important contribution to model refinement and caribou conservation.

5) *Bear predation.* Potential effects of black bear predation (*Ursus americanus*) on caribou need to be examined in field experiments. Although there is evidence that black bears prey on caribou (Ballard 1994), the information on black bear population dynamics in Alberta is scanty, and the effects of black bear predation on caribou populations are poorly understood.

6) *Snow conditions* may affect caribou mobility (Schneider *at al.* 2000) and this could increase caribou vulnerability to predation (Thomas 1995). Some authors (Adamczewski *et al.* 1988, Brown and Theberge 1990, Kelsall and Telfer 1971, Thomas 1995) point out that snow conditions may play important role in caribou population dynamics. Yet, there is a lack of data on the effects of snow conditions limiting caribou access to forage in the boreal ecosystem. Research examining how snow cover influences caribou food habits and energetics would facilitate assessment of the impact of winter conditions on caribou demography.

7) *Predator – prey interactions*. Models attempting to describe predator – prey interactions are based on assumed numerical and functional responses of predators to prey availability. I think that the key elements in wolf (*Canis lupus*) population ecology are wolves' functional response, social spacing behavior (territoriality and pack structure), reproductive potential, and possible prey switching. Although the literature on the above topics has grown in recent years (Eberhardt 1998; Eberhardt and Peterson 1999; Ballard et al. 1987; Fuller 1989; Gasaway et al. 1992; Hayes and Harestad 2000a, 2000b; Hayes et al. 2000; Messier 1985, Messier 1994; Messier and Crete 1985; Messier and Joly 2000), the understanding of the aforementioned factors and their interactions is relatively poor and evidence is sometimes inconsistent (Hayes and Harestad 2000a, Messier 1994). A better understanding of the processes that determine population dynamics of predators is important.

5.2. Ideas for adaptive management

Adaptive management is a basic principle of the Boreal Caribou Committee strategy (BCC 2001). Based on my simulation experiments, I propose the following actions that can be tested in field experiments to validate REMUS outputs and to test the safety and efficacy of a variety of management actions. The most promising and practical strategies could then be implemented in adaptive management at an appropriate scale under the BCC:

1) In Chapter 4 I argued that wolf control is not a viable solution in caribou conservation. Simulations suggested that even if significant reductions of wolves (by 50%) were implemented, the hypothesized thresholds for industrial linear corridors could be exceeded on some caribou ranges. In the absence of wolves and assuming that caribou avoided human-built structures, the maximum hypothetical threshold for seismic lines on caribou range was around 1.6 km/km^2 in simulations with no roads and less than that with roads (around 1.1 km/km^2 of seismic lines with 0.1 km/km^2 of roads). In some caribou ranges the density of linear corridors is close to this threshold (Dyer 1999). Simulation experiments revealed that significant reductions in moose numbers in areas where caribou are being managed could be more beneficial to caribou than direct wolf control. Testing this hypothesis by reducing moose populations on upland areas located within caribou ranges could provide new insights in caribou conservation.

2) Based on my modeling assumptions, I speculate that the thresholds for industrial development on some caribou ranges in northern Alberta may already be exceeded – the model predicts that in areas with around 1.2 km of linear corridors per km^2 (1.19 km/km^2 of seismic lines, and 0.04 km/km^2 of roads) caribou numbers would be reduced by 50% in 15 years, and the species would be extirpated in less than 40 years. Therefore, immediate changes in land use practices and wildlife management actions would be needed. The most beneficial to caribou seem to be all management practices that reduce caribou avoidance of industrial infrastructure. The thresholds for industrial activity suggested by the simulations could be used when establishing habitat targets in caribou conservation. Habitat targets are defined by the BCC as the amount of effective habitat that must be present in boreal caribou ranges in order for caribou populations to be stable or increasing (BCC 2001). The thresholds suggested by REMUS (Chapter 4) could be tested by monitoring caribou population dynamics in areas with known density of linear corridors and oil wells under specific predation pressure and ecosystem carrying capacity.

3) Increasing awareness on caribou conservation could reduce human-caused caribou mortality due to hunting/poaching. Moreover, if humans were not perceived as predators caribou may habituate to human presence. Thus, increased human activity on linear corridors might reduce predation (if wolves avoided humans, and given that people neither hunt nor poach). Monitoring human access in caribou range is one of the key concerns of the BCC in access management (BCC 2001).

5.3. Conclusion

The recommendation of significant reductions of moose based on REMUS simulations is also reinforced by James (1999) who stressed that "it will be difficult to balance the desire to conserve caribou with the desire for increased moose populations". He also stated that because of strong public opposition wolf control is not a viable option. The outputs of the simulation experiments show that even significant reductions in wolf numbers not accompanied by changes in land-use practices would not stop the predicted caribou declines.

Dyer (1999) demonstrated that a significant portion of caribou habitat might be lost due to reduced use of good quality habitat in proximity of industrial infrastructures. He pointed out the lack of research on the effects of the observed avoidance behavior on caribou demography. My work suggests that the functional loss of habitat is the most detrimental factor for caribou dynamics and stressed the importance of more research on the mechanism governing avoidance.

Some of the research I propose has already started or is planned by the Boreal Caribou Research Program (BCRP): avoidance of low-impact seismic lines, use of post-fire habitats, and recovery of existing seismic lines. Moreover, existing research findings can serve as a base for new initiatives. Dyer's (1999) results combined with research on caribou habitat use (Anderson 1999, Bradshaw 1994, Bradshaw *et al.* 1995, Stuart-Smith *et al.* 1997), the Spatial Separation Hypothesis (James 1999) and distribution of caribou and wolves in relation to linear corridors (James 1999, James and Stuart-Smith 2000) could serve as an excellent base for building simulation models of caribou population dynamics that would include habitat heterogeneity and

the effects of landscape on caribou distribution and factors that shape caribou population dynamics.

Significant research on caribou ecology accomplished by the BCRP researchers and numerous current research initiatives (BCRP 2000) will increase the understanding of the boreal ecosystem. Research and experiments suggested in this chapter would enhance the precision of REMUS outputs and advance our understanding of caribou ecology. Extensive knowledge of the boreal ecosystem combined with the will to conserve caribou from all partners in the BCC process, should allow the species to remain part of the boreal ecosystem. MacDonald's (2001) conclusion that most of his respondents from industry and government favored the management options that minimized the cumulative impacts of industry on caribou range show that there is the will to conserve caribou in Alberta.

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